

University of Alberta

Effects of Canada bluejoint grass competition, N fertilization, and litter layer removal on soil N
processes and tree growth

by

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A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the

requirements for the degree of *Master of Science*

in

Soil Science

Department of *Renewable Resources*

Edmonton, Alberta

Fall 2005



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Abstract

The mechanisms of Canada bluejoint grass (*Calamagrostis canadensis* (Michx.) Beauv.) competition is not well understood. I examined the effects of competition, N fertilization, and litter layer removal on soil N processes and the growth of planted white spruce (*Picea glauca* (Moench.) Voss). Weed and litter removal increased soil temperature and net N mineralization and nitrification rates. Litter removal increased litter decomposition rates, probably due to increased soil temperature. Weed control significantly increased tree diameter growth, and foliar N concentration and content. Mineral N supply rates and tree diameter growth were positively related in the field experiment. I conclude that weed control and litter removal had positive effects on increasing N availability and applying N fertilizer without weed control was inefficient in improving tree growth. A complimentary growth chamber experiment showed that sufficient moisture availability might enhance the competitiveness of bluejoint for limited N.

Acknowledgements

Many thanks are extended to Carmela Arevalo, Dr. Woo-Jung Choi, Kirsten Ketilson, Dr. He Liang, Peter Presant, Dan Saurette, Xiao Tan, Kaimin Zhan, and Dr. Huanchao Zhang, for assistance in the field and laboratory. Especially, I appreciate the help from Dr. Woo-Jung Choi who was a great mentor. I would like to thank Dr. Simon Landhäusser for consultation on the growth chamber experiment. I sincerely thank my committee members, Drs. Scott Chang, Phil Comeau, and Vic Lieffers, for their guidance in this entire study. In particular, I would like to thank my supervisor Dr. Scott Chang for his continuous encouragement and guidance throughout the whole process of this thesis research.

I also would like to thank Dave Swindlehurst, Weyerhaeuser Company Ltd., and Paul Godin, Millar Western Forest Products Ltd., for assistance in site selection and in providing information on site history. I thank the Faculty of Graduate Studies and Research and the Department of Renewable Resources, University of Alberta, Natural Science and Engineering Research Council (NSERC) of Canada, the Canadian Foundation for Innovation, the Weyerhaeuser Company Ltd., and Weldwood of Canada Ltd. for funding the research.

Finally, I would like to thank my parents, Kanako and Hitomi Matsushima, and my brother Hirohisa for their understanding, continuous encouragement, and support.

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Chapter 1: Introduction

Canada bluejoint grass (*Calamagrostis canadensis* (Michx.) Beauv., hereafter referred to as bluejoint) is a widespread grass species in the forest understory in North America north of 35° latitude ranging from Newfoundland to Alaska (Hitchcock 1971). Bluejoint has plentiful blades, and their height generally reaches 60 – 120 cm. The characteristic feature of this grass is an underground rhizomatous root system, which is extensive, fibrous, and shallow (Tesky 1992). Bluejoint is a graminoid, sod-forming, cool-season grass (Tesky 1992). Its regeneration mainly takes place from the rhizomes as each node can produce shoots and establish new clones (Lieffers et al. 1993). Bluejoint is dominant or codominant in early successional to climax stages in riparian and cool, moist forest communities (Tesky 1992) such as pine, spruce, and mixedwood stands. This grass also occurs over open uplands and marshy sites (Beckingham et al. 1996). Bluejoint is very drought-resistant once established, although it prefers imperfectly to moderately drained soils (Province of British Columbia 2000). Abundant growth of bluejoint is found in nutrient-rich, moist, and fine to sandy-textured soils with a relatively high water table; good growth of rhizomes occurs in soils with an organic layer (Province of British Columbia 2000; Lieffers et al. 1993).

Bluejoint competes with planted tree seedlings in the early stages of succession (Lieffers et al. 1993). Due to significant economic losses in the forest industry that can be caused by bluejoint (Eis 1981), methods for controlling its vigorous growth are needed. Its growth can be controlled by herbicides (Conn and Deck 1991), mowing, grazing, and mechanical site preparation (Lieffers et al. 1993). Even though social concerns regarding herbicide use have become greater (Imo and Timmer 1998), herbicide application is the

most effective and economical way of controlling this grass.

Bluejoint creates a thick litter layer, a "multi" (Hogg and Lieffers 1991), that is made up of dead shoots that can remain on the soil surface for several years without being decomposed. Litter layers can reduce soil temperature because of their insulating effects. Hogg and Lieffers (1991) found that mean soil temperature during summer at 10 cm depth averaged 3.8 °C cooler in soils under shoots and litters of bluejoint.

Lieffers et al. (1993) defined four successional stages to describe the ecology of bluejoint: closed canopy, newly disturbed, grass-dominated sites, and transition to trees and shrubs. In sites newly disturbed by fire or clear-cutting, bluejoint starts its recruitment by expanding its rhizomes. Within 3 years after a disturbance, bluejoint can become a dominant species in a site. At this stage, the detrimental effects of bluejoint on tree growth are significant (Conn and Deck 1991; Lieffers et al. 1993; Ländhausser and Lieffers 1998; Robinson et al. 2002). Bluejoint is one of the most competitive species in boreal forest ecosystems in western Canada (Robinson et al. 2002).

This study aims to improve our understanding of nitrogen (N) cycling processes and plant nutrition in a spruce plantation infested by bluejoint in the boreal forest in northern Alberta. Improving our understanding of the ecology of bluejoint is critical in the successful management of this competitive weed species in boreal forests. The following five points further justify the research conducted in this study:

1. Whether N or moisture deficiency is the main limiting factor for tree growth is poorly understood when trees are associated with bluejoint. Nitrogen is often the most deficient nutrient and significant moisture deficiency can occur in boreal forests.

2. Many studies on bluejoint competition have been carried out in forests within a few years after disturbance or in pots where the length of study was only a few months. However, bluejoint may still be a problem beyond the initial stand establishment phase.
3. Even though the importance of belowground competition has been increasingly recognized, there is little evidence to show that there is a relationship between belowground resource reduction caused by bluejoint competition and tree growth performance. Also, the effects of bluejoint proliferation on soil N cycling have not been studied in detail.
4. The importance of the litter layer formed by accumulated dead bluejoint shoots in insulating soil temperature has been recognized; however, the effects of the litter layer on microbial activities and N cycling in the soil have not been studied.
5. The interactions between water and N availabilities on the competitive ability of bluejoint have not been studied.

I conducted a field and a pot experiment to address some of the questions raised above. The objective of the field study was to examine the effects of bluejoint control, N fertilization, and litter layer removal on soil N cycling and tree growth in a young white spruce (*Picea glauca* (Moench.) Voss) plantation. The pot experiment was conducted to determine the interaction between water and N availabilities on competitive abilities of bluejoint and white spruce for N. White spruce was used in these experiments because it is a main commercial tree species commonly planted on sites prone to bluejoint infestation in Alberta. The following four hypotheses were tested in this study.

1. Bluejoint competes for N with white spruce and at the same time reduces net N mineralization and net nitrification rates in the soil, thereby reducing N availability and tree growth.
2. The litter layer of bluejoint reduces soil temperature, N mineralization rates, and N availability, leading to reductions in tree growth and N uptake.
3. Nitrogen fertilization increases soil N availability and tree growth.
4. Bluejoint requires sufficient amounts of available water for its optimal N uptake and for maintaining its competitiveness. Thus, when there is insufficient available water, bluejoint becomes less competitive for N uptake. When soil water is sufficient, bluejoint out-competes white spruce even though there is insufficient nitrogen because of the extreme ability of bluejoint to take up N.

This thesis consists of five chapters. This chapter is an introduction to the whole thesis. The next chapter (Chapter 2) reviews the literature related to weed competition, litter layer effects, and N cycling in boreal forests. Hypotheses 1, 2, and 3 were tested in the field experiment, and are discussed in Chapters 3 and 4. The last hypothesis was tested in the pot experiment that is reported in Chapter 5. The last chapter (Chapter 6) provides synthesis of the two experiments and general conclusions.

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Chapter 2: Literature review

2.1 Mechanisms for the strong competitiveness of bluejoint

Canada bluejoint grass (*Calamagrostis canadensis* (Michx.) Beauv., hereafter referred to as bluejoint) is one of the most competitive species in boreal forests (Lieffers et al. 1993). Bell et al. (2000) noted that immediately after the establishment of plant communities the herbaceous species had greater competitiveness than woody plants. Bell et al. (2000) also cited the more rapid occupation of growing space by bluejoint as the main reason for its high competitiveness.

The morphological traits that give competitive advantages to bluejoint have been widely discussed, i.e., the strong rhizome system that is important both as a storage site for carbohydrates and as an organ for clonal expansion (Powelson and Lieffers 1992). The rhizomes are responsive to high light and nutrient conditions, so new plants can be recruited immediately after a forest disturbance (Powelson and Lieffers 1992), allowing bluejoint to quickly become a dominant species and sometimes a solo species making up the plant community in sites that have recently been disturbed (Lieffers et al. 1993).

Another morphological characteristic that may facilitate the competitiveness of bluejoint is a thick litter layer that is made up of dead shoots that may remain on the soil surface for several years without being decomposed (Hogg and Lieffers 1991). Hogg and Lieffers (1991) found that the mean soil temperature during summer at 10 cm depth averaged 3.8 °C cooler in soils underneath bluejoint than in the control. Tryon and Chapin (1983) reported negative responses of white spruce (*Picea glauca* (Moench.) Voss) and other taiga tree species roots to reduced soil temperature at 10 cm depth. The

growth of aspen (*Populus tremuloides*) was reduced as soil temperature decreased from 20 to 12, and from 12 to 6 °C (Ländhausser and Lieffers 1998). On the other hand, the growth of bluejoint did not respond to temperature treatments (9 and 21 °C), even though its competitiveness was reduced slightly by the temperature reduction (Ländhausser and Lieffers 1994), suggesting that bluejoint may out-compete tree species by lowering soil temperature as a result of its thick litter layer.

The litter layer of bluejoint may have allelopathic effects. A pot experiment that placed dead shoots of bluejoint on soil surface showed a significant growth reduction for aspen, especially when nutrient supply to aspen was low (i.e., as a second stress factor) (Ländhausser and Lieffers 1998). This finding suggests a strong implication for an allelopathic effect of bluejoint, even though more conclusive evidence to confirm the effect is not yet available.

Besides the morphological characteristics of bluejoint, high competitiveness for belowground resources such as mineral N and soil moisture has been used to explain the dominance of bluejoint (Robinson et al. 2001). A study using ¹⁵N-labelled fertilizer in the first 2 years of succession in the boreal region showed that grass species, mainly bluejoint and fireweed (*Epilobium angustifolium*), were able to absorb a significant amount of broadcast-applied N fertilizer regardless of whether mechanical site preparations were used. Results showed that ¹⁵N uptake by white spruce was very small; fertilizer use efficiency of grass spp. was 1.85 and 0.68%; and white spruce was 0.10 and 0.36% after the first and second growing seasons, respectively (Staples et al. 1999). By using controlled-release fertilizer (CRF), this unwanted N uptake by competing weed species can be minimized (Hangs et al. 2003a). However, Hangs et al. (2003a) stated that bluejoint could successfully compete with planted conifer seedlings for the applied

fertilizer-N despite the placement of the fertilizer bags close to tree seedlings. Hangs et al. (2003a) also reported improved biomass growth and N status of pine and spruce seedlings through vegetation management, a result which clearly indicates the strong competitive ability.

In agreement with these studies, a hydroponic study that quantitatively measured NH_4^+ and NO_3^- uptake by roots of several boreal forest species (fireweed, white spruce and jack pine (*Pinus banksiana*)) showed the high N uptake ability of bluejoint (Hangs et al. 2003b). Bluejoint used N from solutions much more quickly than all the other studied species. Also, bluejoint was able to take up NH_4^+ and NO_3^- simultaneously, while white spruce and jack pine had a limited ability for NO_3^- uptake and a slower rate of uptake for NH_4^+ . A study by Hangs et al. (2002) confirmed that N limited the growth of white spruce and jack pine seedlings in pots when they are associated with bluejoint. Finally, it was concluded that the ability of bluejoint to produce greater root densities with its fibrous root system (i.e. a morphological attribute), along with its efficient N uptake system (i.e. a physiological attribute), gives some understanding of bluejoint's high competitiveness for N with conifer seedlings (Hangs et al. 2002).

Bluejoint can reduce tree growth through affecting the physiological conditions of trees such as reduced photosynthesis rates, N concentrations, nitrogen-use efficiency (NUE), and water-use efficiency (Robinson et al. 2001). Meanwhile, bluejoint NUE increased throughout the season, and ammonium nitrogen (NH_4^+) in soil was significantly reduced when the density of bluejoint was increased. There was a correlation between jack pine photosynthesis rate and NH_4^+ and NO_3^- availability; thus, Robinson et al. (2001) stated that N uptake by bluejoint might have played an important role in the reduced growth of jack pine.

2.2 Mechanisms of plant competition

The establishment of understory vegetation (e.g., grass vegetation) after a disturbance plays an important role in nutrient retention, soil erosion control, and wildlife forage supply in forest ecosystems. However, understory vegetation often has serious detrimental effects on crop trees especially in the early stage of succession and results in economic losses in commercial forests and agroforestry systems (Eis 1981; Nambiar and Nethercott 1987; Campbell et al. 1994; Mead et al. 1993).

Many attempts have been made to provide a precise and meaningful definition of competition. Mead and Mansur (1993) defined competition in forests as: "a result of a combination of factors responsible for tree growth associated with understory vegetation in ecosystems." This definition in particular seems to apply to the competition between bluejoint and trees. Casper and Jackson (1997) explained resource-mediated competition that occurs belowground and causes a negative effect on the availability of some resources to which another plant shows a positive response in growth, survival, or reproduction. This relationship between plants and resources is depicted in Figure 2.1 (Casper and Jackson 1997). Obviously, competition plays an important role in determining vegetation structure in plant communities and involves a multitude of organisms and complex interactions (Nambiar and Sands 1993).

The main resources necessary for plant growth are light, nutrients, and water. Competition for light can be categorized as a form of aboveground competition, while competition for nutrients and water can be termed belowground competition. Light is the ultimate source of energy for any forest ecosystem; it provides the energy for photosynthesis and the signals used in the photo-regulation of plant growth and

development. There are at least 20 essential mineral nutrients required for plant growth, with nitrogen (N) being the most common limiting in temperate forests (Fisher and Binkley 2000). The supply of soil moisture, which is sometimes very limited due to relatively low precipitation in boreal forests, largely controls species composition in plant communities because water is essential to the proper functioning of most plant processes (Fisher and Binkley 2000).

Inter-specific competition, including competition between crop trees and weeds, should be considered as important as intra-specific competition in forest ecosystems (Nambiar and Sands 1993). In the boreal forest region, at least 17 plant species, for example bluejoint and fireweed, are serious competitors against outplanted jack pine and black spruce (Bell 2000). They successfully compete for resources with trees in early successional stages from planting to canopy closure (Nambiar and Sands 1993).

2.2.1 Belowground resource movement and competition

When a plant takes up nutrients from soil solutions or soil surfaces, plant roots must come into contact with the nutrient ions. There are three ways to achieve this: root interception, mass flow, and diffusion. These processes are important in plant competitiveness for nutrients. Root interception is the capture of nutrients and water when the root system comes into contact with them, and it can be enhanced by the growth of new roots and by mycorrhizal associations (Casper and Jackson 1997; Havlin et al. 1999). As root volume is generally small in soils, the amount of nutrient absorbed by this process is very small (Casper and Jackson 1997). Mass flow and diffusion are the main mechanisms for nutrient movement in soils (Van Rees et al. 1994). Mass flow is the

nutrient movement in soil water as a result of plant transpirational water uptake, evaporation, and percolation of soil water (Casper and Jackson 1997; Havilin et al. 1999). Therefore, the amounts of nutrients that can be delivered to the root surface are dependent on the rate of water flow (water consumption by plants) and the average nutrient concentrations in the soil solution. This process is more important for mobile nutrients such as NO_3^- than for immobile ones. Diffusion, the movement of an ion from an area of higher to an area of lower concentration, occurs when nutrient uptake of plants exceeds the supply of nutrients by mass flow (Casper and Jackson 1997). Competition for belowground resources occurs when a root's zone of influence begins to encroach on the resources of neighboring roots (Van Rees et al. 1994). Therefore, diffusion is the most important process in nutrient movement in the soil (Casper and Jackson 1997). A steep nutrient gradient may indicate a high degree of competition. Larger gradients may be created for immobile nutrients. More intensive competition may occur for immobile nutrients such as phosphorous and NH_4^+ .

Competition for water is extremely important but is still poorly understood (Casper and Jackson 1997), although numerous studies have been conducted that manipulated water availability, vegetation density, and species compositions (Nambiar and Sands 1993). Generally, there are strong consistent negative influences of competing vegetation on water availability for crop trees (Nambiar and Sands 1993).

The availability of water to plants is determined by soil and plant water potential and soil hydraulic conductivity, which is strongly related to water potential and water-filled pore space (Fisher and Binkley 2000). Therefore, studies of competition for water usually involve the measurement of water potential. However, since water availability in soil is not the same phenomenon as competition intensity (Casper and

Jackson 1997), plant water potential is used as an indicator of water stress caused by competition (e.g., Nambiar and Zed 1980). Nambiar and Zed (1980) found that when a competing species was not controlled, the leaf water potential of trees was very low, indicating water stress caused by competition.

Interactions between soil moisture and nutrients are critical in understanding plant competition since mass flow and diffusion of nutrients occur in soil solutions as discussed above, but many competition studies fail to take them into account simultaneously. As Nambiar and Sands (1993) explain: "it is possible that most studies attributing the competition effects on tree growth mainly or exclusively to water have failed to account for the possible simultaneous effects of changing nutrition on growth. To an extent, the opposite may be the case in field studies that examined only nutrition, without considering water availability." Therefore, it is important to consider that soil water deficits, as a result of competition, can affect soil nutrient availability, tree nutrient uptake, and tree nutrition. For example, Blank et al. (2002) studied the mechanisms of competitiveness for broadleaved pepperweed (*Lepidium latifolium*), which mainly invades wetland and riparian zones, and found that biomass growth was facilitated under high soil water potential. They concluded that this species invades moisture-rich environments because high soil water content allows efficient transport of nutrients to the well-established root system. While competition for water may dominate the early years after tree planting, competition for nutrients may become more critical in later years (Nambiar and Sands 1993).

2.2.2 Competitive abilities of plants

According to Nambiar and Sands (1993), competitive plants in inter-specific competition can: 1) obtain a larger amount of water and nutrients, 2) utilize these resources more efficiently to produce biomass than other plants, and 3) strategically allocate assimilated resources to maximize their survival rates. The first requirement can be achieved through morphological and physiological attributes. Since nutrient uptake takes place on plant root surfaces, the root surface area may correlate with the relative nutrient uptake of the plant. However, this is not always the case due to intra-specific competition, spatial and temporal variations in nutrients, mycorrhizal activities, and the physiological properties of plant nutrient uptake (Casper and Jackson 1997). Other morphological traits such as relative growth rate, biomass production, fine root density, and total root surface area are important in determining a plant's ability to occupy space at the initial stage of plant competition (Casper and Jackson 1997). Space itself is sometimes mentioned as a resource, but its status seems to be controversial (Nambiar and Sands 1993).

The second requirement is achieved through high nutrient- and water-use efficiencies. These components will be discussed in detail later in this review. The third requirement can be represented by N allocation to photosynthetic tissues in the form of enzymes (Casper and Jackson 1997) and carbohydrates, that is, energy reserves in root systems. Usually, the allocation of carbohydrates is a plant strategy that enables it to be ready to proliferate following a canopy removal.

2.2.3 The effects of soil nutrient gradients on competition

The effects of the addition of limiting nutrients or soil nutrient gradients lead to a controversial topic: whether fertilization increases or reduces the intensity of belowground competition in forest ecosystems and whether it even exacerbates competition (e.g., Campbell et al. 1994). Grubb (1994) summarized the nature of the paradox of belowground competition. He used 'competition' to describe the condition in which two organisms or two species take up the same resources from a common pool, concluding that, in this sense, competition may or may not lead to competitive detrimental effects. Because of the fact that experimental results sometimes differ between field and greenhouse studies, two extreme environmental conditions were used to clearly understand the paradox: 1) the soil being initially devoid of living roots, and 2) the soil having reached a steady state in terms of the amount of fine roots.

The first situation can be found in the initial stage of forest succession right after a disturbance or in pot experiments starting with growing media without plants in them. Under these conditions, the plant that is going to invade a newly disturbed site should be able to vigorously compete for nutrients and water by having longer or a greater number of roots (especially fine roots) and taking up nutrients more quickly per unit time than other species. Therefore, the higher relative growth rate (RGR) (greater biomass production per unit plant weight) that enables the plants to occupy growing space initially is critical because obtaining space directly influences the ability to capture resources. Occupation of space by competing species excludes the roots of other plant species. In this case, any additional fertilization cannot improve the situation or may even make it worse because added nutrients are simply absorbed by the competing species and

converted into its biomass. Plants established in such a nutrient-rich site will dominate until the overstory of trees is established. However, competition is less intensive in nutrient-poor sites.

The second environment can be found in the later stage of forest succession after sufficient establishment of root systems. In this situation, the key trait of competitiveness is the ability to reduce the mean concentration of limiting nutrients in soil solutions. This is achieved by a plant having a high rooting density or physiological abilities, particularly the ability to absorb nutrients of extremely low concentration. In this scenario, a species that requires very small amount of resources can be competitive in nutrient poor sites, and the chances of invasion by species requiring a large amount of nutrients are very low.

2.3 Interactions between plant species and soil N cycling

Plant species can influence soil N processes and N availability (Scott and Binkley 1997; Scott et al. 2001; Knops et al. 2002). And these impacts on soil N cycling, in turn, have effects on the ability of the species to compete with other species (the invasibility of the species) (Ehrenfeld 2003). The pathways for a plant species to alter N cycling in a system are, for example, pools of aboveground and belowground biomass, net primary productivity, chemical composition of biomass, and rates of litterfall (Blank et al. 2002; Wallstedt et al. 2002).

Having a unique N use efficiency (NUE) is one of the ways for a plant species to alter N cycling (Knops et al. 2002). Berendse and Aerts (1987) stated that NUE essentially has two components: 1) the mean residence time of nitrogen in the plant, i.e., the period during which the absorbed N can be used for carbon fixation, and 2) the

instantaneous rate of carbon fixation of the plant per unit of N (PNUE, photosynthesis N use efficiency). Plants with longer mean residence times may have a competitive advantage due to efficient biomass production, especially under nutrient poor conditions. Similarly, in relation to competition for N between a plant and soil microbes, the plant can be more competitive due to its longer N-retention period than that of soil microbes, even though the plants have a small portion of available N (Kaye and Hart 1997). Also, a plant with higher nitrogen productivity can be more competitive under relatively nutrient rich conditions because it can respond rapidly to increased nutrient availability (Berendse and Aerts 1987). Longevities of tissues and PNUE are different between species (Knops et al. 2002); therefore, species-specific NUE can cause a unique impact on N cycling.

Changes in N cycling processes belowground occur through alterations in the soil microbial community in response to different quantities and qualities of nutrient inputs by different plant species (Ehrenfeld 2003). The processes that can be affected by inputs of a plant species and, at the same time, can affect plant growth are N mineralization, immobilization, and nitrification (consequently nitrate leaching) (Figure 2.2). In particular, changed microbial activities exert a significant influence on N mineralization (Knops et al. 2002).

In Figure 2.2, the plants input litter, roots, and exudates (A), and some plants also can produce allelochemicals (A'). Pathway B is known as N mineralization: decomposition of soil organic matter into mineral N by heterotrophic organisms (Havlin et al. 1999). Ammonium may be oxidized by autotrophic nitrifiers and become nitrate (pathway C), and this is defined as nitrification. Mineral N can also be assimilated into soil microbial organisms (pathway D), and this is defined as immobilization. The plants

can have impacts on soil N cycling such as B, C, and D through the pathway A and A'. For example, inputting plant tissue that has high quality (low C:N ratio), due to high N availability, can accelerate rates of N mineralization and thus lead to higher N availabilities (Knops et al. 2002). Similarly, litter quality, which is defined as lignin:N ratio, can control net N mineralization (Scott and Binkley 1997). Plant roots can influence soil N processes through changing oxygen partial pressure and providing C-sources through their exudates (e.g., Le Roux et al. 2003). Exudates of plant roots stimulate soil microbial activities such as N mineralization since those exudates are C (energy source) rich (Tate 2000). Allelochemical inputs may directly impact on soil N cycling such as N mineralization (Souto et al. 2000), N immobilization (Bowman et al. 2004), and nitrification (Vitousek and Matson 1985). Nitrification is known to be inhibited by allelochemicals (Vitousek and Matson 1985). Since the soil N processes are driving forces to provide plant available N, these changes caused by plants have the potential to affect competitive interactions between the species affecting environments and other species (e.g., Bowman et al. 2004).

Ehrenfeld (2003) summarized 79 papers on the effects of exotic plant species invasion on soil nutrient cycling processes and found that invasions have been associated with increases (9 out of 21 cases), decreases (6 out of 21), and no changes (6 out of 21) in total soil N. It seems that no clear tendency emerged; however, 10 studies found increased microbial biomass N (MBN), mostly associated with increased total soil N. Extractable inorganic N (NH_4^+ and NO_3^-) also did not show a clear trend. But it was common that N mineralization and nitrification increased in response to invasions (11 out of 16 cases). These changes have been attributed to differences in the amount and spatial distribution of soil microbial biomass (MB) and fine roots and differences in the N

concentration in litter. In addition to changes in nutrient cycling, soil moisture content, water flow pattern, and soil evapo-transpiration are decreased or increased by exotic species, depending on the plant size, leaf area, and rooting density of the species and environment. Ehrenfeld (2003) claimed that these changes might improve the invasibility of ecosystems and the invasiveness of the exotic species.

Kalmia (*Kalmia angustifolia*) has been demonstrated to have detrimental effects on black spruce growth (Wallstedt et al. 2002). The study found that total N (% of soil dry mass) in the F horizon increased as the *Kalmia* cover class became greater. The H horizon also showed similar results, even though they were not statistically significant. The authors stated that these N increments indicate immobilization of N in the organic layer. The dominant pathway of soil N cycling shifted from mineral to organic forms, which are more recalcitrant complexes. *Kalmia* can take advantage of the organic form of N over other plant species (tree seedlings) under this condition because it is considered to have a greater capacity to use organic N through ericoid mycorrhizas associated with its roots (Wallstedt et al. 2002).

2.3.1 Tree growth may depend on soil N availability

In resource-mediated belowground competition, resource availability affects the growth of competing plant species, and competing species change resource availability (Casper and Jackson 1997). As a result of competition for N, target plant growth sometimes depends on N availability, which can be reduced by competing vegetation (Hangs et al. 2004). The changed plant community, as a result of competition, alters soil processes and thus N availability, facilitating the competitive ability of a species

(Ehrenfeld and Scott 2001). In forest ecosystems, N availability in soils is driven by the processes of decomposition and N mineralization in the surface soil and litter layer in combination with large amounts of C that was fixed by trees (Attiwill and Adams 1993). And soil MB may play an important role in N availability for plants or decomposers.

Even though the importance of organic N uptake by plants has been increasingly recognized (Schimel and Bennett 2004), net N mineralization rates have been widely accepted as an index of plant available N supply rate since they correlate strongly with plant N uptake (Kaye and Hart 1997). Soil microbial organisms can be a sink or source of nutrients, and plants and soil microbes can be in intensive competition for mineral N, and microbes can release mineral N only when there is an excess amount of mineral N in the soil (Kaye and Hart 1997). This concept led to the development of methodologies to measure net N mineralization rates, which are estimations of the release of mineral N from soil organic matter, determined by several methods such as the buried bag and core sampling techniques (Eno 1960; Raison et al. 1987). Such methods have been widely adopted in competition studies. These methods, however, have a disadvantage: they do not take into account N uptake of plant roots, and thus the N supposed to be taken up by plants sometimes is taken up by microbes during incubation, causing negative annual net N mineralization rates (immobilization by soil microbes) (Schimel and Bennett 2004). The technique using ion-exchange membrane to determine N availability is relatively new and is believed to solve some of the above problems (Qian and Schoenau 2001). Hangs et al. (2004) found significant correlations between tree growth measurements and N availability measured by ion-exchange membranes, where N availability was likely to be reduced by competing vegetation.

The soil microbial population regulates the decomposition of organic materials

and nutrient transformations (Franzluebbers 1999). Microbial biomass is storage of labile N, and the mineralization of MBN can contribute a significant portion of plant N requirements (Carter et al. 1999). The chloroform fumigation-extraction (CFE) method is widely used to measure MB in acidic forest soils (Brookes et al. 1985; Vance et al. 1987).

In forest systems infested by a major weed species, N mineralization and MB may be largely affected by this species through plant residue input to the soil. For example, Scott and Binkley (1997) suggested that plant litter lignin:N ratio can be used as a general predictor of net N mineralization rates. Lignin:N ratio is species-specific, and it seems to regulate net N mineralization rates. Therefore, in a system experiencing severe competition, competing species can have a significant impact on net N mineralization rates as compared with non-infested areas. Prescott et al. (2000) investigated differences in net N mineralization rates in stands associated with different tree species. They found that net N mineralization rates in the forest floor were affected more significantly by understory vegetation composition than tree species composition. In addition, characteristics of plant species, especially their net primary production and litter input, can affect MB, which is a driving factor in soil processes including N mineralization (e.g. Carter et al. 1999). Whether the effects are positive or negative is dependent upon decomposability and the N content in litter (litter quality). Plant root activity is also important to soil microbial activities, but their relationships remain unclear (Carter et al. 1999).

2.3.2 The effects of N fertilization on N mineralization, MB, and plant competition in forests

In N-limited ecosystems such as in the boreal forest region, inadequate available N in soils often reduces crop tree growth. To remediate this situation, forest management practices such as N fertilization are applied. Despite the frequent use of N fertilization in forests, the efficiency of fertilization is not clear (Staples et al. 1999). In these systems, soil microbes and trees both lack N, so that applied N often stimulates microbial N uptake and respiration (Fisk and Fahey 2001). Consequently, MB and net N mineralization rates are reduced (Fisk and Fahey 2001). But the responses to N application vary depending on other environmental conditions. Short-term responses to the added N include the "priming effect" (Kuzayakov et al. 2000). According to a review by Kuzayakov et al. (2000), mineral-N fertilizers possibly cause acceleration of soil organic matter mineralization by lowering C:N ratio and providing substrates and energy source. This result can cause either positive or negative feedback for microbial activities.

Some studies used ^{15}N -labeled fertilizers to track the fate of N fertilizer in forest ecosystems with strong competition from understory vegetation (Chang et al. 1996b; Chang and Preston 2000; Staples et al. 1999). Chang et al. (1996a) found that understory competition was stimulated as a result of N fertilization and that resulted in reduced growth of crop trees. Staples et al. (1999) found that removal of understory vegetation increased the fertilizer-use efficiency of white spruce seedlings by limiting competition for N. Also, they stated that fertilizer was immobilized fairly quickly in the soil under N limiting conditions. However, understory vegetation can positively affect microbial biomass growth and thus increase nutrient retention. For example, Busse et al. (1996)

found a significant reduction in microbial biomass C (MBC) associated with a long-term (35-yr) absence of understory vegetation.

2.4 Measurements of tree stresses caused by understory species competition

Traditional competition indices such as Lorimer's index, spacing factor, and basal diameter ratio are widely used to predict the performance of crop trees as a function of interference from a localized subset of unwanted plants based on individual tree measurements. However, these indices take into account only aboveground measurements and they do not explain competition mechanisms; they do not distinguish the limiting factor of tree growth that are caused by competition, i.e., moisture or/and nutrient(s) deficiencies (Mead and Mansur 1993). Foliar analysis has been used to assess nutrient status affected by silvicultural treatments such as herbicide and fertilizer applications (Haase and Rose 1995). Vector analysis has been developed to examine fertilization effects on tree growth (Timmer and Stones 1978). Vector analysis is comparatively new and has only recently been adopted to test the type of interaction between plants, particularly competition effects on trees (Mead and Mansur 1993; Imo and Timmer 1998 and 1999), called vector competition analysis. Vector competition analysis as outlined by Mead and Mansur (1993) involves foliar nutrient analysis and biomass determination only for trees, while the method by Imo and Timmer (1998 and 1999) requires the determination of both trees and unwanted vegetation response to vegetation management. These methods can indicate the types of effects of understory species on tree growth in forests, whether they would be antagonistic, compensatory, or synergistic effects. Also, they provide estimation of possible interaction effects, such as

those related to nutrients, moisture and/or light competition.

Figure 2.1 The Relationship between resource availability and plant competition (Casper and Jackson 1997).

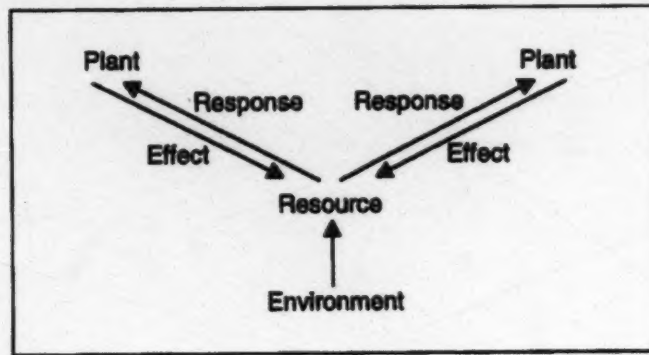
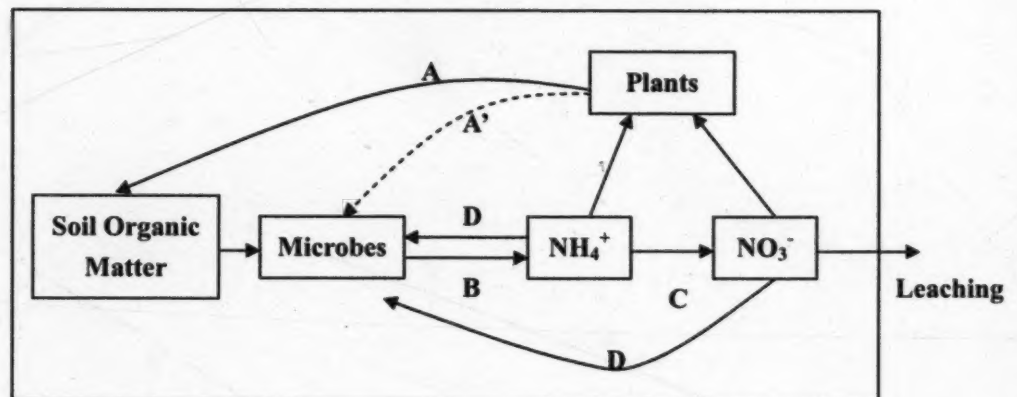


Figure 2.2 A conceptual model that shows an effect of plants on soil microbial activities through organic matter input (A) or direct effect (A'). The affected soil N processes are N mineralization (B), nitrification (C), and immobilization (D).



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Chapter 3: Effects of weed control, N fertilization, and litter layer removal on N cycling in a 13-year-old white spruce plantation

3.1 Introduction

Canada bluejoint grass (*Calamagrostis canadensis* (Michx.) Beauv., hereafter referred to as bluejoint) is a highly competitive native grass species in boreal forests in northern Alberta. Bluejoint can have detrimental effects on tree growth which result in serious economic losses to the forestry industry, as severe weed competition can delay forest regeneration (Lieffers et al. 1993). To improve forest management practices in areas prone to bluejoint competition, many studies have been conducted regarding the mechanisms of competition for this species (Eis 1981; Ländhausser and Lieffers 1998; Bell et al. 2000). However, most previous studies have focused on aboveground competition rather than belowground processes that affect N availability, which is considered most limiting in boreal ecosystems (Kimmins 1996). Bluejoint also creates a thick litter layer made up of dead shoots that can remain on the soil surface for several years without being decomposed. The litter layer reduces soil temperature because of its insulating effect (Hogg and Lieffers 1991). The effects of the litter layer on soil processes that control N availability have not received much attention. Therefore, a better understanding of soil N cycling in systems associated with bluejoint will help us understand the mechanisms of the competitiveness of bluejoint.

Herbicide application (hereafter referred to as weed control) is a common silvicultural tool that is used to control competition from understory weeds in forest ecosystems. Weed control has been reported to increase soil moisture content as a

consequence of eliminating moisture uptake by understory weeds and to increase soil temperature due to increased solar radiation reaching the soil surface (Reynolds et al. 2000; Gurlevik et al. 2004). Microbial biomass C (MBC) usually decreases after repeated applications of herbicide due to reductions in input of labile C from root exudates, fine root mortality, and leaf and litter fall leachates (Ohtonen et al. 1992; Perie and Munson 2000; Li et al. 2004). On the other hand, the short-term effect of weed control on MBC was not significant in another study (Houston et al. 1998). Net N mineralization and nitrification rates have been reported to increase after weed control (Reynolds et al. 2003; Li et al. 2003; Gurlevik et al. 2004). Reduction of plant N uptake may lead to greater nitrification rates since plants and nitrifiers compete for NH_4^+ (Zak et al. 1990; Lavoie and Bradley 2003).

Microbes can immobilize exogenous mineral N while decomposing organic matter, resulting in reduced N availability that can limit microbial activities and growth (Kaye and Hart 1997). Nitrogen application can increase MBC and microbial biomass N (MBN) in N limited soils (Hart and Stark 1997; Compton et al. 2004). However, N fertilization sometimes suppresses microbial activities and reduces microbial biomass (Thirukkumaran and Parkinson 2000; Compton et al. 2004). This suppression may be due to the changes of microbial community structure (Compton et al. 2004) or other reasons (reviewed by Fog 1988). In relatively young forest stands, net N mineralization and nitrification rates increase after N application (Ohtonen et al. 1992; Gurlevik et al. 2004), but Fisk and Fahey (2001) found increased gross N immobilization with low gross N mineralization after N application and suggested that N application increased the physiological activity and N demand of soil microbes.

The objective of this study was to examine the effects of bluejoint control, N

fertilization, and litter layer removal on soil N cycling and white spruce growth. This chapter focuses on the effects of weed and litter removal and N application on soil temperature, moisture content, and N cycling processes and soil properties such as mass loss rate of litter, microbial biomass C (MBC) and N (MBN), net N mineralization, net nitrification, and available N.

3.2 Materials and methods

3.2.1 Study site

The study site (54°07'20.7"N, 115°50'09"W) was located approximately 20 km south west of the city center of Whitecourt in Alberta. It was located within the Forest Management Area (FMA) of Millar Western Forest Products Ltd. The study site belongs to the Lower Foothills Natural Subregion (Beckingham et al. 1996) of the Boreal Plain Ecozone (Ecological Stratification Working Group 1996). The average annual precipitation from 1971 to 2000 recorded by the Environment Canada weather station in Whitecourt (54° 8' N, 115° 47' W) was 578 mm (352 mm occurred in the summer between June and September); the average snowfall was 178 cm; the mean annual temperature was 2.6 °C (13.4 °C in summer) (Environment Canada 2004a). The mean temperatures in summer 2003 and 2004, when this experiment was conducted, were 14.0 and 13.2 °C, respectively; the summer precipitation in 2003 and 2004 was 141 and 358 mm, respectively (Environment Canada 2004b). In this region, the average annual potential evapotranspiration is 508 mm (The National Atlas of Canada 1974).

The stand was clear-cut in November 1991, and white spruce was then planted

in 1992. Herbicide was sprayed to control understory vegetation in 1996 and 2000. The average height and diameter of white spruce trees in 2003 in the experimental plots are shown in Table 3.1. In June 2003, the understory of the site was heavily infested by bluejoint (50 to 100% cover; Table 3.1). Also, there was a significant amount of bluejoint dead shoot (litter) accumulation on the ground (Table 3.1). Where the site was less infested by bluejoint, there was relatively more fireweed.

The parent material of the soil series is lacustrine, and the site lies in an undulating topography (Wynnkyk et al. 1969). The soil in the study site was classified as an Eluviated Sombric Brunisol according to the Canadian System of Soil Classification (Soil Classification Working group 1998). The soil drainage class was determined as moderately well to imperfectly drained; the soil texture of the Ae horizon was silt-to-silt loam based on manual texturing. The forest floor and mineral soil (0-10 cm depth) of each experimental plot were initially characterized for pH and total C and N using samples collected on June 5, 2003 (Table 3.2).

3.2.2 Experimental design

Three treatments were applied to 24 experimental plots in a 2 x 2 x 2 split-split plot design with 3 replications (3 blocks). Boundaries between the experimental plots were at least 3 meters. The factors applied to the experiment are described in Table 3.3.

Each experimental plot was 8 x 8 m and included 5 to 14 trees. The block boundaries were delineated parallel to the plantation rows. A few naturally regenerated lodgepole pine seedlings were found in some of the treatment plots. They were manually removed from the established experimental plots. The establishment of the weed

removal treatment was completed by clipping live grasses in early June 2003 and herbicide (glyphosate) application in late June and July 2003. Herbicide was again applied in early August 2004 because in some experimental plots weed sprouts were found. Glyphosate application at the rate of expected field concentration should have little or no effect on soil microbial communities (Busse et al. 1996). For the second treatment, urea 200 kg N ha^{-1} was broadcast on the plots on June 5, 2003. To establish the litter removal treatment, bluejoint litter was manually cut and removed out of the experimental plots on June 5, 2003. The amount of litter removed was weighed with a hand-held digital scale and then dry matter removed was calculated based on moisture content of the litter material. In the second year, litter was found to accumulate in the weed intact and litter removed plots and was cut and removed (the amount was not determined at this time) from these plots on June 7, 2004.

3.2.3 Soil sampling and measurements

Soil sampling: Soil sampling was conducted at multiple points in time: on June 5, June 22, July 22, August 25, and September 28 in 2003; on June 7, July 7, August 6, and September 7 in 2004. Within each experimental plot, four soil samples were collected from randomly selected points and combined to form a composite sample for the forest floor and 0-10 cm mineral soil. A soil core was collected using a stainless steel bulb planter (10 cm long and 5 cm diameter), and forest floor (hereafter referred to as LFH) and mineral soil (0-10 cm) were separately collected from the same core. Soil samples were preserved in coolers and transported back to the lab, and they were immediately put in a refrigerator (4°C) until further analysis. The initial soil samples collected on June 5,

2003, were used to determine soil pH and total C and N concentrations. After each sampling, soil samples were sieved and homogenized, and plant roots were removed in the lab and analyzed for the following parameters.

pH: Air-dried LFH and mineral soil samples were used to determine pH, using 1:10 (w/v) and 1:2 soil to water ratios for LFH and mineral soil (Thomas 1996), respectively. Soil pH was measured using a pH meter (719 S Titrino, Ω Metrohm, Brinkman, Switzerland). Data were averaged by blocks since the samples were collected before the treatments were applied (Table 3.2).

Total C and N concentrations: Air-dried LFH and mineral soil samples were used to determine total C and N concentrations using a Shimadzu TOC-V CSH/CSN Total Organic Carbon and Total N Analyzer and SSM-5000A Solid Sample Module (Shimadzu Corporation, Kyoto, Japan). Carbon concentration was divided by N concentration to obtain the C:N ratio.

Soil temperature: Soil temperature at 10 cm from the mineral soil surface was recorded by HOBO[®] H8 Temp Loggers (Onset Computer Corporation, Bourne, MA, USA) in the two growing seasons; two loggers were buried in each experimental plot on June 25, 2003 and June 7, 2004. The hourly readings from the loggers were averaged to calculate the daily means for each plot. Furthermore, growing season (93 days in 2003 and 92 days in 2004) means were calculated and used for statistical analysis. Three loggers in 2003 and one logger in 2004 out of 48 were lost. In these cases, the values from the single remaining datalogger were used.

Moisture content: Gravimetric moisture contents of LFH and mineral soils were determined by drying them in an oven at 65 and 105 °C, respectively, using about 5 g fresh LFH and 20 g fresh mineral soil.

Litter decomposition rate: The decomposition rate of bluejoint litter was measured using the litter bag method. Dead shoots of bluejoint were collected near Edson and Drayton Valley in May 2003. The litter was dried in an oven at 70 °C for 24 hours, cut into pieces about 5 cm long, and then mixed well. The homogenized litter sample contained 43% C and 0.64% N and was defined as the original litter. Approximately 5 g of the litter was weighed and placed into a nylon mesh bag that had a 1 mm opening and a 400 cm² area. In total, 9 litter bags were placed in each experimental plot on June 22, 2003; 3 bags were placed on ground surface on each of the 3 locations within each plot. One bag from each of the 3 locations, and, therefore, three bags within each plot, were retrieved on July 22, September 28, 2003, and September 7, 2004, respectively. The collected litter bags were dried in an oven at 70 °C for 24 hours and cleaned using a brush. The rate of litter decomposition (%) was calculated by the following formulae:

Litter decomposition rate measured as percent mass loss =

$$[\text{Weight loss during the measurement period} / \text{Initial weight of litter}] \times 100$$

Decomposition constant (k) was determined to evaluate decomposability of litter. K-values were calculated by fitting the following model to the overall mean across the treatments in each sampling date.

$$X_t = X_0 e^{-kt}$$

where X_t is the weight of averaged litter weight remaining after the decomposing period, X_0 is the weight of initial litter, and t is time expressed in year.

Soil microbial biomass C (MBC) and N (MBN): Soil microbial biomass was determined using the fumigation-extraction method (Vance et al. 1987) for all the soil samples except for the samples collected on July 7 and Sept 7, 2004. Chloroform-fumigation was conducted for 24 hours, and it was followed by extraction with 50 mL 0.5 M K_2SO_4 and filtration using filter papers (Fisherbrand® Q2 filter paper). For LFH, 10 g fresh samples were fumigated, so that on a dry-matter basis, approximately a 1:5 (w:v) ratio was used for the extraction. For mineral soil, 13-15 g of fresh samples were fumigated, and, therefore, a ratio of 1:10 (w:v) was used. Non-fumigated samples were also extracted in the same manner without fumigation. Both extracts were stored in plastic bottles in a freezer (-18 °C) before further analysis. The concentrations of dissolved organic C and N in the extracts were determined by a Shimadzu TOC-V CSH/CSN Total Organic Carbon and Total N Analyzer (Shimadzu Corporation, Kyoto, Japan). The values were then calculated to convert them to biomass as follows:

$$MBC (\text{flush}) = [TOC (\text{fumigated}) - TOC (\text{non-fumigated})]$$

$$MBN (\text{flush}) = [TN (\text{fumigated}) - TN (\text{non-fumigated})]$$

Soil net N mineralization and nitrification rates: Soil samples were incubated in four randomly selected points as intact cores in plastic bags in-situ to determine net N mineralization and nitrification rates (Eno 1960) for about one month 3 times each year. Soils from four points made up a composite sample in each experimental plot. Fresh samples before and after incubation (5 g LFH and 10-13 g mineral soils) were extracted using 50 mL 0.5 M K₂SO₄. They were filtrated using Fisherbrand® Q2 filter paper. Extracts were stored in plastic bottles in a freezer (-18 °C) until further analysis. Ammonium (NH₄⁺) concentration of the extracts was determined by the modified indophenol blue method (Mulvaney 1996); nitrate (NO₃⁻) concentration was determined by the vanadium (III) chloride method (Doane and Horwath 2003); and the absorbance was measured by a spectrophotometer (Genesys 10-S, Thermospectronic, USA). Net N mineralization and nitrification rates were calculated using the following formulae:

$$\text{Net N mineralization rate} = ([\text{NH}_4^+ + \text{NO}_3^-]_t - [\text{NH}_4^+ + \text{NO}_3^-]_0) / t;$$

$$\text{Net nitrification rate} = ([\text{NO}_3^-]_t - [\text{NO}_3^-]_0) / t;$$

where t is the number of days the sample was incubated. Incubations were conducted in 2003 and 2004, but only the result for 2004 is given bellow, as I believe the 2003 rates were adversely affected by the heterogeneity created by fertilizer N application. Incubations were conducted three times from June 7 to July 7, from July 7 to August 6, and from August 6 to September 7. These dates are abbreviated as June, July, and August, respectively, hereafter.

Mineral-N concentrations: NH_4^+ and NO_3^- concentrations in LFH and mineral soil were determined as described for soil net N mineralization and nitrification. This is a measure of soil N availability and was measured on un-incubated samples.

Potential N supply rate of soils: Plant Root Simulator (PRS)TM-probes (Western Ag Innovations Inc., Saskatoon, Canada), which were equipped with ion-exchange membranes, were used to estimate the potential N supply rates of the soils to plants. Four cation and four anion probes saturated with sodium (Na^+) and bicarbonate (HCO_3^-), respectively, were inserted into the soil in each experimental plot and incubated for one month. A probe was buried so as to make approximately half of the area of the membrane in contact with LFH and the other half in contact with mineral soil. After a 30-day insertion period, the probes were taken out of the soil and then in the identical place, the same type of probe (anion or cation) was inserted to start another incubation. The probes were buried from June 7 to July 7, July 7 to August 6, and August 6 to September 7, each period hereafter being referred to as June, July, and August insertions. The NH_4^+ and NO_3^- ions captured by the ion-exchange membranes of the four sets of anion and cation probes that were retrieved from each experimental plot were extracted by 0.5 N HCl, and the concentrations of mineral N were determined colorimetrically by an autoanalyzer (The Technicon Auto Analyzer, 1977).

3.2.4 Statistical analyses

The PROC MIXED procedure in SAS (version 8.2, SAS Institute Inc., Cary, N. C.) was used to analyze soil moisture content, MBC and MBN, litter mass loss rates, net

N mineralization and nitrification rates, mineral-N concentrations, and potential N supply rates. The data concerning LFH and mineral soil were analyzed separately. Also, the data in 2003 and 2004 were separately analyzed. Outliers were assessed by plotting the data as a scatter plot. Normality tests on the data set conducted using the PROC UNIVARIATE procedure (the Shapiro-Wilks test) showed that most of the time, transformations of data were not required. However, the Bartlett test using the PROC GLM procedure showed that the data had variances that were not homogenous. The PROC MIXED procedure overcomes this problem. Because the data had only 3 replications, there were not enough degrees of freedom to test more than 3-way interactions. Also, the 3-way interactions in this study can be difficult to interpret. Therefore, in the statistical model, the main factors and the 2-way interactions were included. For statistical significance, $\alpha = 0.05$ was chosen.

3.3 Results

3.3.1 Soil temperature

Soil temperature at 10 cm depth was significantly increased by weed and litter removal in both 2003 and 2004, but fertilization did not affect soil temperature (Figure 3.1). Averaged summer temperature was increased 0.73 °C by weed removal and 0.93 °C by litter layer removal in 2003, and 0.73 °C by weed removal and 0.59 °C by litter removal in 2004. Weed and litter removal significantly interacted with time to affect soil temperature. The temperature change caused by the treatments from July 1st to August 31st was greater than in the rest of measured period. From July 1st to August 31st in 2003,

weed removal increased soil temperature by 0.80 °C, and litter removal increased by 1.13 °C. In the same period in 2004, weed and litter removal increased soil temperature by 0.92 °C and 0.57 °C, respectively. The combination of weed and litter removal appear to be additive.

3.3.2 Gravimetric soil moisture contents

In 2003, weed removal increased soil moisture contents in both LFH ($p < 0.001$) and mineral soil ($p < 0.001$), and in LFH, litter removal decreased moisture content ($p = 0.001$) (Table 3.4, Figure 3.2). In 2004, soil moisture contents were not affected by any of the treatments, probably because 2004 was a wetter year.

3.3.3 Litter decomposition rate

The average rate of mass loss of bluejoint litter 1, 3, and 15 months after exposing to the soil decreased with time. The decomposition constant, k -value, was 0.35 ($R^2 = 0.985$). In the first month, 11.2% (w:w) of the litter was decomposed, followed by 20.6% at 3 months and 42.4% at 15 months on average (Figure 3.3). The rate of decomposition was fastest in the first month, and then gradually declined. The rate was also increased by N fertilization ($p = 0.014$ at 3 month; $p = 0.007$ at 15 months) and litter removal ($p < 0.001$, Table 3.5), and the effects were clearest in the last measurement (at 15 months). Since the positive effects of N fertilization and litter removal were additive, the highest decomposition rate was observed in the Wr-N200-Lr treatment.

3.3.4 Soil microbial biomass C and N

The effects of weed and litter removal on MBC and MBN were inconsistent among different sampling times (Figure 3.4 and 3.5). In LFH, N fertilization usually decreased MBC, and the opposite effects were frequently found in mineral soil; however, these effects were not statistically significant (Table 3.5). In 2003, MBN in LFH was significantly reduced by N fertilizer ($p = 0.020$, Table 3.5). The MBN of mineral soil showed a trend similar to that of LFH, but it was not significantly different among the treatments (Table 3.5).

3.3.5 Net N mineralization and nitrification rates

The first year results (3 samplings in July, August, and September 2003) of net N mineralization and nitrification rates were greatly affected by sampling time, and inconsistency of the trend made it difficult to interpret the data (data not shown). This result might have reflected the increased heterogeneity of soil N dynamics resulting from fertilization. The first year results are excluded in this section. Net N mineralization rates were significantly correlated with soil temperature at 10 cm depth (LFH: $R^2 = 0.311$, $p < 0.001$; mineral soil: $R^2 = 0.149$, $p = 0.001$) (Figure 3.6 and 3.7, Table 3.6). The seasonal changes in mineralization rates in LFH and mineral soil were similar to each other; N immobilization was found in June, and the greatest mineralization rates were found in July. Also, the Wr-N200-Lr usually showed the highest rate of mineralization among the treatments. In LFH, litter removal increased net N mineralization rates ($p = 0.017$), and weed removal and fertilizer application increased net N mineralization of mineral soil (p

< 0.001; $p = 0.002$, respectively, Table 3.6). Analysis of the significant weed removal by fertilization interaction indicates that the degree of positive effect by N fertilization was much greater when weed was removed than when weed was intact.

Net nitrification rates had very similar trends to those of net N mineralization rates (Figure 3.6 and 3.7). Net nitrification was affected by sampling time in mineral soil ($p < 0.001$, Table 3.6); the greatest nitrification rates were observed in the July incubation period (Figure 3.7). N fertilization increased the nitrification rates in LFH ($p = 0.002$). This was also found in mineral soil ($p = 0.001$), and, additionally, weed removal increased nitrification rates ($p < 0.001$, Table 3.6). Weed removal and N fertilization interactively increased net nitrification rates of mineral soil ($p = 0.006$); the effect of N fertilization on nitrification rates was accelerated by weed removal. N fertilization did not increase nitrification rates where weed vegetation was intact.

3.3.6 Soil mineral N concentrations

The concentrations of NH_4^+ and NO_3^- in LFH and mineral soil were more variable in the earlier stage of the experiment, when N fertilizer was just applied (Figure 3.9 and 3.10). Variations among replications were also large. In fertilized plots, since the form of fertilizer was urea, NH_4^+ was the main mineral-N observed at the beginning of the experiment (June to August in 2003), and the concentrations tended to be higher in weed-removed and litter-intact plots. Then, gradually NO_3^- concentrations increased due to nitrification. The highest NO_3^- concentration was found in September 2003. When weed was intact and N was applied, the reduction in NH_4^+ concentrations with time was faster than in weed removed and N applied plots. Weed removal significantly increased

soil NO_3^- concentration in 2004 (LFH: $p = 0.001$ and mineral soil: $p = 0.010$, respectively; Table 3.4). The interaction of these factors was also significant (LFH: $p = 0.007$; mineral soil: $p = 0.001$; Table 3.4).

3.3.7 Potential N supply rate

The potential N supply rate in the LFH-mineral soil interface to plants was determined using PRSTM-probes in 2004 (Figure 3.11). Whereas the K_2SO_4 -extracted NO_3^- was usually larger than NH_4^+ , NO_3^- captured on the PRSTM-probe was more than 10 times larger than that of NH_4^+ . This is probably due to the higher mobility of NO_3^- in soils. The seasonal change was found only for NO_3^- ($p = 0.004$; Table 3.6); the amount of captured NO_3^- slightly decreased with time. Weed removal increased the amount of NH_4^+ captured on the PRSTM-probe ($p = 0.046$). On the other hand, NO_3^- was influenced by weed removal, fertilization, and their interaction ($p < 0.001$, $p = 0.013$, and $p = 0.020$, respectively). The interaction was exactly the same as the one for K_2SO_4 -extracted NO_3^- ; the N fertilization effect was prominent only when weeds were removed.

3.4 Discussion

3.4.1 Soil temperature and gravimetric moisture content

Hogg and Lieffers (1991) reported that soil temperature at 10 cm depth was 3.8 °C lower in plots infested with bluejoint than in mowed plots due to the insulation effects of accumulated dead and standing shoots of bluejoint. They observed that removal of the litter layer without removing new shoots that emerge in summer significantly increased

soil temperature. This study also found that removal of either living or accumulated litter of bluejoint significantly increased soil temperature. However, the temperature increase was much smaller in this study: the combination of removing living shoots and the litter layer increased soil temperature by only 1.4 °C compared with the control on average across 2-year results. A possible reason for those differences may be that the measurement of soil temperature only started in June in our study; Hogg and Lieffers (1991) found relatively large temperature increases by bluejoint removal from April to May. In this study, the greater effects of weed and litter removal on soil temperature were observed in July and August. Also, the thickness of litter layer should be compared when we compare the intensity of the insulation effect. The amounts of accumulated litter in this site and the one of Hogg and Lieffers (1991) were similar (579 and 527g m⁻², respectively). However, in my study litter layer was compressed by experimenters stepping on the research plots in the later stage of the experiment since this field study involved repeated soil and plant sampling. Higher soil moisture content in 2004, which would increase the soil heat capacity, may be another factor contributing to a reduction of these differences. Due to these reasons, the insulation effect of the litter layer might have been reduced, causing smaller increases caused by litter removal in 2004 than in 2003.

Nitrogen fertilization did not affect soil temperature. The response of bluejoint biomass to N fertilizer in the first year appeared to be positive but non-significant in 2004 (Figure 4.4a). The amount of N fertilizer used in this study was not enough to increase bluejoint biomass production for more than 1 year and thus failed to cause an impact on soil temperature.

Soil gravimetric moisture content has been reported to increase by removing understory vegetation in forest ecosystems, leading to increased leaf water potential of

trees (Karl and Doescher 1993; Paris et al. 1998). Therefore, changes in soil gravimetric moisture content could be an indication of competition intensity for soil moisture among plants. Robinson et al. (2001) reported that soil volumetric moisture content at 45 cm depth decreased with the increment of bluejoint density. In this study, soil gravimetric moisture content in both LFH and mineral soil (0-10 cm) was significantly decreased by bluejoint infestation in 2003 (Figure 3.2). The high amount of precipitation in 2004 might have muted the negative effects of weed infestation on moisture contents and caused differences between 2003 and 2004 with regards to the effects of weed and litter removal.

3.4.2 Litter decomposition

A decomposition constant (k-value) of 0.35 for bluejoint was relatively low compared with other grass species, such as 1.36 for prairie grass litter (initial 1.07% N) in Saskatchewan (Köchy and Wilson 1997) and 1.39 for grass species (initial 0.89% N) in southern Alberta (Taylor et al. 1989). In this experiment, bluejoint litter had lower N concentration (0.64%) and relatively higher C:N ratio (63) compared with other grass species (e.g., Smith and Bradford 2003). Low N concentration often causes slow decomposition (Taylor et al. 1989; Aerts 1997; Köchy and Wilson 1997; Smith and Bradford 2003). Lignin:N ratio also has been reported to control the rate of litter decomposition (Aerts 1997). In this study, lignin concentration in bluejoint was not measured. The slow rate of litter decomposition is one of the reasons for the accumulation of a thick layer of bluejoint litter in the studied stand. Also, the low k-value and high C:N ratio of litter suggest that N taken up by bluejoint has a relatively long

mean residence time in undecomposed litter.

Usually, litter decomposition rate is affected by environmental factors such as soil moisture content and temperature (Aerts 1997), and decreased soil moisture causes decreased decomposition rates (Slamanca et al. 2003). However, in this study, litter removal, which decreased soil moisture content in 2003, increased decomposition rate, indicating that the negative effect of reduced moisture content in the weed and litter removed plots may be cancelled out by the continuously increased soil temperature (Figure 3.3). Köchy and Wilson (1997) reported a similar result that the highest decomposition rate was found in open prairie among the combination of shading (open or artificially shaded) and location (forest or prairie), indicating that soil temperature may have played an important role in litter decomposition.

Smith and Branford (2003) found that the decomposition rate of grass litter with higher N was higher, but this effect appeared only after 60 days when the litter was in smaller mesh sized bag. They concluded that micro-fauna could not be mobile to seek high quality litter until they grow and colonize. In this study, most likely added N decreased C:N ratio of LFH and litter in litter bags and stimulated the mineralization of litter, and this phenomenon appeared to be more apparent at 3 months when soil micro- and meso-fauna colonized and reached the litter material having increased N availability.

3.4.3 Soil microbial biomass C and N

Soil microbial populations, measured as microbial biomass C (MBC) and N (MBN), regulate nutrient cycling processes in terrestrial ecosystems (Franzluebbers 1999). The mineralization of MBC and MBN can contribute a significant portion of plant

N requirements (Carter et al. 1999). At the same time, soil microbial populations can limit plant available N due to their ability to immobilize N (Schimel and Bennett 2004). The amount of MBC can be affected by environmental factors (such as soil moisture content and temperature), organic matter content, and plant-related attributes (e.g., litter quality, root exudates) (e.g., Bardgett et al. 1999; Chen et al. 2003). In most cases, MBC shows seasonal changes (Wardle 1998; Chen et al. 2003). In this study, MBC and MBN in LFH and mineral soil significantly fluctuated with sampling time (Figure 3.4 and 3.5). A regression analysis showed that moisture content was positively related to MBC in LFH ($R^2 = 0.51$, $p < 0.001$, data not shown) and mineral soil ($R^2 = 0.133$, $p < 0.001$) and MBN in LFH ($R^2 = 0.294$, $p < 0.001$), while soil temperature did not show any relationship. MBN was also correlated (LFH: $r = 0.213$, $p = 0.01$; mineral soil: $r = 0.391$, $p < 0.001$) with 0.5 M K_2SO_4 extractable organic C (data not shown). MBC was correlated with extractable organic C in mineral soil ($r = 0.206$, $p = 0.015$). It can be concluded that MBC and MBN changed seasonally due to changes in soil moisture content, which may be caused by changes in precipitation and plant uptake. However, soil organic C is also an important driving factor of changes in microbial population size.

Soils with understory vegetation tend to have higher MBC due to higher soil organic C content caused by litter input and root turnover (Ohtonen et al. 1992; Amatya et al. 2002). On the other hand, Houston et al. (1998) reported that vegetation management using glyphosate in clear-cut stand in Ontario did not change MBC or organic matter content after 2 years of the herbicide application. In this study, the increased extractable organic C in the weed removal treatment can be hypothesized to be originated from dead roots of weeds that did not affect MBC content. Soil microbial biomass growth, therefore, can be limited by other factors such as N availability other

than C (energy) supply.

Nitrogen fertilization tended to negatively affect MBC and MBN in LFH but positively or did not affect MBC and MBN in mineral soil (Figure 3.4 and 3.5). The reported effects of N addition on microbial biomass and activities in forest soils are contradictory; i.e., the effects can be positive or negative (Compton et al. 2004). In terrestrial ecosystem, there is a competition for N between plants and microbes, and lack of N can limit soil microbial activity (Kaye and Hart 1997). Nitrogen addition to N limited environments can increase microbial population size and activities (Compton et al. 2004). Opposite effects are also frequently found, as summarized by Fog (1988). For example, Thirukkumaran and Parkinson (2000) observed suppressed microbial activities (microbial respiration and substrate induced respiration (SIR)) caused by the application of ammonium nitrate and urea. Also, Compton et al. (2004) found that 11 years of chronic addition of ammonium nitrate to a forest soil decreased soil microbial biomass C.

In this study, increased N immobilization and C assimilation may have resulted in increased MBC in the mineral soil since mineral N content in boreal forest ecosystems is usually very low. On the other hand, N addition negatively affected MBC for LFH. Fog (1988) suggested that negative effects of added N on microbial biomass are mainly found in soils with recalcitrant organic matter with high C:N ratio, supported by the higher C:N ratio in LFH than in mineral soil (Table 3.2) and much higher C:N ratio (63) for bluejoint litter. According to Fog (1988), the possible explanation for this suppression effect caused by added N can be: (1) disturbance of the competition between potent and less potent decomposers; (2) blocking of production of certain enzymes; and (3) amino compounds condense with polyphenols and other decomposition products, which can be toxic or inhibitory. The study of Thirukkumaran and Parkinson (2000) conducted in a

laboratory showed enhanced $q\text{CO}_2$ by the addition of urea (188 kg N ha^{-1}). They suggested that microbes utilized C inefficiently in fertilized soils (more C was used per unit MBC). Experiencing this change in substrate utilization after N fertilization, microbial activities could remain unchanged or enhanced. Compton et al. (2004) found that 11 years of chronic addition of ammonium nitrate to a forest soil decreased MBC and also altered the composition of microbial community (DNA profiles). In this study, decreases in MBC and MBN with N fertilization in LFH were most likely due to changes in microbial community structure and its population caused by N addition. In mineral soil, N application tended to increase MBN because of increased microbial immobilization of

3.4.4 Net N mineralization and nitrification rates

The in-situ buried bag method (Eno 1960) used in this study excludes the contact of plant roots to mineral-N in the soil incubated in a plastic bag and provides a measure of the net N mineralization rate, which is a balance between gross rates of N mineralization and N immobilization by microbes (Hart et al. 1994), is an estimate of plant-available N (Tate 2000). Even though net N mineralization rates were close to negative values in June, the high net nitrification rates at this time showed that there was a substantial amount of released nitrate (Figure 3.6 and 7). This result indicates that ammonium was intensively immobilized by microbes. This tendency disappeared in July and August.

In the LFH horizon, net nitrification rate was increased by N fertilization (Figure 3.7), and this occurred because the availability of substrate for nitrifiers was increased.

Substrate limitation for nitrifiers can be caused by uptake of NH_4^+ by plants or soil heterotrophs (Zak et al. 1990). Litter management did not have any effect on nitrification. And nitrification did not have a relationship with soil temperature ($R^2 = 0.002$; $p = 0.716$). Weed control has been reported to increase net nitrification in other studies (e.g., Reynolds et al. 2000). The increment in net nitrification caused by weed removal in this study appeared more dramatically in mineral soil. Since soil temperature at 10 cm depth showed a significant relationship with the net nitrification rate in mineral soil ($R^2 = 0.177$, $p < 0.001$), indicating that soil temperature may have been a factor influencing nitrification rate, as reported by Reynolds et al. (2000). A previous study noted that allelochemicals can inhibit nitrification (Vitousek and Matson 1985), and bluejoint litter has a potential to be allelopathic (Landhausser and Lieffers 1998).

3.4.5 Extractable ammonium and nitrate concentration

Ammonium concentrations in fertilized plots were markedly decreased within 3 months after fertilization in 2003 in both weed intact and weed-removed plots. Therefore, ammonium was consumed by both bluejoint and microbial immobilization. The ability of bluejoint to take up ammonium and nitrate was higher than white spruce (Hangs et al. 2002). Nitrate produced through nitrification was likely to be taken up by bluejoint since little amount of nitrate was found in weed intact plots. In 2004, differences in $[\text{NH}_4^+]$ between weed intact and weed-removed plots became much smaller than in 2003. Nevertheless, the concentration of nitrate in weed-removed plots was evidently higher than in weed intact plots. If ammonium and nitrate were mainly taken up by bluejoint, the concentration of mineral N in weed intact plot must have been similarly depleted, or

more severely depleted in ammonium since bluejoint takes up ammonium faster than nitrate (Hangs et al. 2002). However, this was not the case in 2004. It can be possible that there is a competition for ammonium between bluejoint and nitrifiers, ammonium in weed intact plots was mainly assimilated by bluejoint, and ammonium in weed-removed plots was mainly assimilated by nitrifiers. Consequently, a significant accumulation of nitrate was found only in weed-free plots due to the lack of plant uptake and higher production of nitrate. Similar competition for ammonium and superiority of certain plant species for acquiring it have been reported elsewhere (Zak et al. 1990; Kaye and Hart 1997). Also, differences in net nitrification rates support this hypothesis, especially in mineral soil where mineral-N concentration was lower than in LFH.

3.4.6 Potential N supply rate to plants

Potential N supply rate to plants was measured using ion exchange resin, and the technique has advantages over conventional soil extraction methods: ion exchange resin can reflect the factors affecting nutrient uptake by plants such as soil moisture and temperature, mineralization and immobilization, ion diffusion, free ion activities, etc (Qian and Schoenau 2002; Hangs et al. 2004). Ion exchange membrane act as an ion sink, which simulates ion absorption by plant roots (Western Ag Innovations Inc. 2004). Since, in this study, plant roots were not separated from the probes, the measured values are net N supply rates, i.e., total soil supply – plant uptake.

The net supply rates of NH_4^+ and NO_3^- were significantly lower in weed intact plots than in weed removed plots (Figure 3.11), similar to the results of net mineralization rates measured using the buried bag method. The lowered values in weed

intact plots may be due to uptake of plants, immobilization, and low rate of N mineralization. In particular, N uptake by bluejoint appears to be an important factor affecting N availability since it has a much greater maximum uptake value than white spruce (Hangs et al. 2002). Significantly high NO_3^- availability found in weed-removed plots may be a result of increased NH_4^+ availability for nitrifiers where there was no uptake of bluejoint. In addition, N fertilization increased net supply of NO_3^- only when weed was removed. Hydrolysed NH_4^+ from applied urea N in weed intact plots was possibly taken up by bluejoint, with no increment of available NH_4^+ for nitrifiers. Consequently, these results suggest that NH_4^+ is under competition of bluejoint and nitrifiers in weed intact plots. Decreased net N supply by the infestation of bluejoint, found in this study, can be a critical factor that can negatively influence tree growth. The relationship between the net supply rate of mineral-N and tree growth is discussed in Chapter 4.

3.5 Conclusions

Bluejoint and its litter layer were hypothesized to have negative impacts on net N mineralization and net nitrification rates and consequently reduce soil N availability (see Chapter 1). In this experiment, removal of bluejoint vegetation and the litter layer significantly increased soil temperature at 10 cm depth, and this increment was further associated with increased net N mineralization and net nitrification rates. When bluejoint is intact, the activity of nitrifiers may be limited by NH_4^+ availability due to large N uptake of bluejoint or other factors that were not studied. Increased net N mineralization and nitrification rates, as a result of weed removal, may increase N availability for other

plant species such as white spruce. This was supported by the potential N supply rate measured using PRSTM-probes.

It can be concluded that bluejoint infestation changed soil N cycling, particularly reducing N availability for other plant species in a forest ecosystem. Also, bluejoint may affect N cycling through its litter input and accumulation. Compared with previous studies (Köchy and Wilson 1997; Taylor et al. 1989), k-value (decomposition constant) for bluejoint litter was relatively low, and its C:N ratio was high, indicating that N taken up by bluejoint has a relatively long mean residence time. Furthermore, the thick litter layer decreases the decomposition rate of litter, probably due to decreased temperature. Litter layer affected soil moisture content, soil temperature, and N cycling in this experiment. In addition, during dry summers, the presence of bluejoint can reduce soil moisture availabilities.

Table 3.1 The basic characteristics of the vegetation at the study site, determined on July 5, 2003 before fertilizer and herbicide application. (n = 8 within each block; mean $\pm$ SE).

Block	White spruce		Bluejoint	
	Height (cm)	Diameter (cm)	Cover (%)	Litter biomass (g m ⁻²)
1	179 $\pm$ 15	3.7 $\pm$ 0.4	73 $\pm$ 12	461 $\pm$ 124
2	184 $\pm$ 15	3.8 $\pm$ 0.4	87 $\pm$ 13	595 $\pm$ 102
3	180 $\pm$ 12	3.5 $\pm$ 0.3	85 $\pm$ 11	681 $\pm$ 102

Table 3.2 The properties of the studied soil. Soil samples were collected on June 5, 2003 before fertilizer and herbicide application. (n = 8 within each block; mean $\pm$ SE).

Block	Soil horizon	pH _(water)	Total C (%)	Total N (%)	C:N ratio
1	LFH	4.9 $\pm$ 0.2	23.6 $\pm$ 5.1	1.3 $\pm$ 0.4	19.0 $\pm$ 2.3
	Mineral soil	5.2 $\pm$ 0.2	1.4 $\pm$ 0.2	0.1 $\pm$ 0.01	11.1 $\pm$ 1.1
2	LFH	5.2 $\pm$ 0.1	29.3 $\pm$ 3.7	1.3 $\pm$ 0.2	22.5 $\pm$ 2.5
	Mineral soil	5.0 $\pm$ 0.1	1.4 $\pm$ 0.3	0.1 $\pm$ 0.01	11.2 $\pm$ 1.1
3	LFH	5.3 $\pm$ 0.3	29.2 $\pm$ 2.5	1.3 $\pm$ 0.2	23.6 $\pm$ 3.2
	Mineral soil	5.3 $\pm$ 0.1	1.7 $\pm$ 0.22	0.1 $\pm$ 0.01	12.6 $\pm$ 1.1

Table 3.3 Treatments applied in the field experiment and their abbreviations, as used in the thesis.

Factors		
Main plot level	Subplot level	Sub-subplot level
Bluejoint vegetation intact (Weed intact: WI)	No fertilizer application (N0)	Litter layer intact (Li)
Bluejoint vegetation removed (Weed removed: Wr)	Urea N applied at 200 kg N ha ⁻¹ (N200)	Litter layer removed (Lr)

Table 3.4 P values from the analysis of variance using repeated measures for gravimetric soil moisture content, NH_4^+ and NO_3^- concentrations, and soil temperature (0-10 cm depth).

Effect	Moisture				NH_4^+				NO_3^-				Mineral				Temperature			
					LFH								soil							
	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004
Weed control (W)	<0.001	0.152	0.001	0.077	0.001	0.001	0.001	0.001	<0.001	0.113	0.092	0.003	0.457	0.010	0.025	<0.001				
N fertilization (N)	0.194	0.436	<0.001	0.677	0.001	0.371	0.193	0.845	<0.001	0.298	0.411	0.087	0.671	0.194						
Litter removal (L)	0.001	0.387	0.127	0.681	0.446	0.857	0.785	0.706	0.460	0.999	0.306	0.531	0.002	0.001						
W*N	0.274	0.932	0.006	0.219	0.006	0.479	0.952	0.106	0.514	0.506	0.308	0.064	0.685	0.274						
W*L	0.623	0.848	0.037	0.654	0.497	0.813	0.562	0.774	0.374	0.176	0.406	0.501	0.253	0.623						
N*L	0.415	0.474	0.195	0.115	0.174	0.832	0.785	0.427	0.469	0.114	0.418	0.707	0.248	0.415						
Time (T)	<0.001	0.037	<0.001	0.001	<0.001	0.001	<0.001	<0.001	<0.001	<0.001	0.576	0.011	<0.001	<0.001						
W*T	0.055	0.987	0.114	0.972	<0.001	0.001	<0.001	0.893	0.361	0.021	0.388	0.005	<0.001	0.055						
N*T	0.108	0.821	<0.001	0.362	0.001	0.414	0.166	0.928	<0.001	0.035	0.369	0.086	<0.001	0.108						
L*T	0.048	0.863	0.132	0.880	0.183	0.960	0.919	0.421	0.425	0.647	0.408	0.648	<0.001	0.048						

Table 3.5 P values from the analysis of variance for rate of mass loss of litter, and soil microbial biomass C and N.

Effect	Rate of mass loss of litter				MBC		MBN		MBC		MBN		Mineral		Soil	
	1 month	3 months	15 months		2003	2004	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004
Weed control (W)	0.624	0.148	0.406		0.441	0.310	0.560	0.806	0.090	0.252	0.363	0.338				
N fertilization (N)	0.281	0.014	0.007		0.201	0.051	0.020	0.060	0.417	0.368	0.354	0.161				
Litter removal (L)	0.046	0.111	0.001		0.606	0.370	0.123	0.764	0.117	0.368	0.859	0.357				
W*N	0.696	0.514	0.034		0.122	0.732	0.174	0.812	0.316	0.942	0.019	0.650				
W*L	0.499	0.171	0.599		0.432	0.709	0.478	0.367	0.556	0.673	0.867	0.844				
N*L	0.118	0.178	0.414		0.199	0.069	0.356	0.051	0.386	0.404	0.236	0.983				
Time (T)					<0.001	0.300	0.002	0.018	<0.001	<0.001	<0.001	<0.001				
W*T					0.700	0.253	<0.001	0.049	0.047	0.031	0.442	0.050				
N*T					0.231	0.741	0.014	0.686	0.731	0.948	0.310	0.771				
L*T					0.935	0.627	0.882	0.813	0.220	0.193	0.960	0.558				

Table 3.6 P values from the analysis of variance using repeated measures for soil net N mineralization (N Min.) and nitrification rates and potential N (NH_4^+ and NO_3^-) supplies measured by PRS-probes in 2004.

Effect	N Min.		Nitrification		N Min.		Nitrification		PRS- NH_4^+	PRS- NO_3^-
		LFH				Mineral Soil				
Weed control (W)	0.916		0.186		<0.001		<0.001		0.046	<0.001
N fertilization (N)	0.131		0.002		0.002		0.001		0.279	0.013
Litter removal (L)	0.017		0.682		0.531		0.291		0.215	0.260
W*N	0.224		0.204		0.048		0.006		0.544	0.020
W*L	0.126		0.074		0.665		0.205		0.613	0.247
N*L	0.742		0.492		0.786		0.432		0.467	0.948
Time (T)	<0.001		0.448		<0.001		<0.001		0.004	0.127
W*T	0.678		0.043		0.228		0.008		0.757	0.102
N*T	0.330		0.816		0.212		0.015		0.234	0.319
L*T	0.206		0.455		0.270		0.543		0.630	0.364

Figure 3.1 Daily mean soil temperature at 10 cm depth in the mineral soil for (a) summer 2003 and (b) summer 2004, as affected by weed and litter removal. The data for N0 and N200 were averaged as fertilization had no effect on soil temperature. The abbreviations are given in Table 3.3.

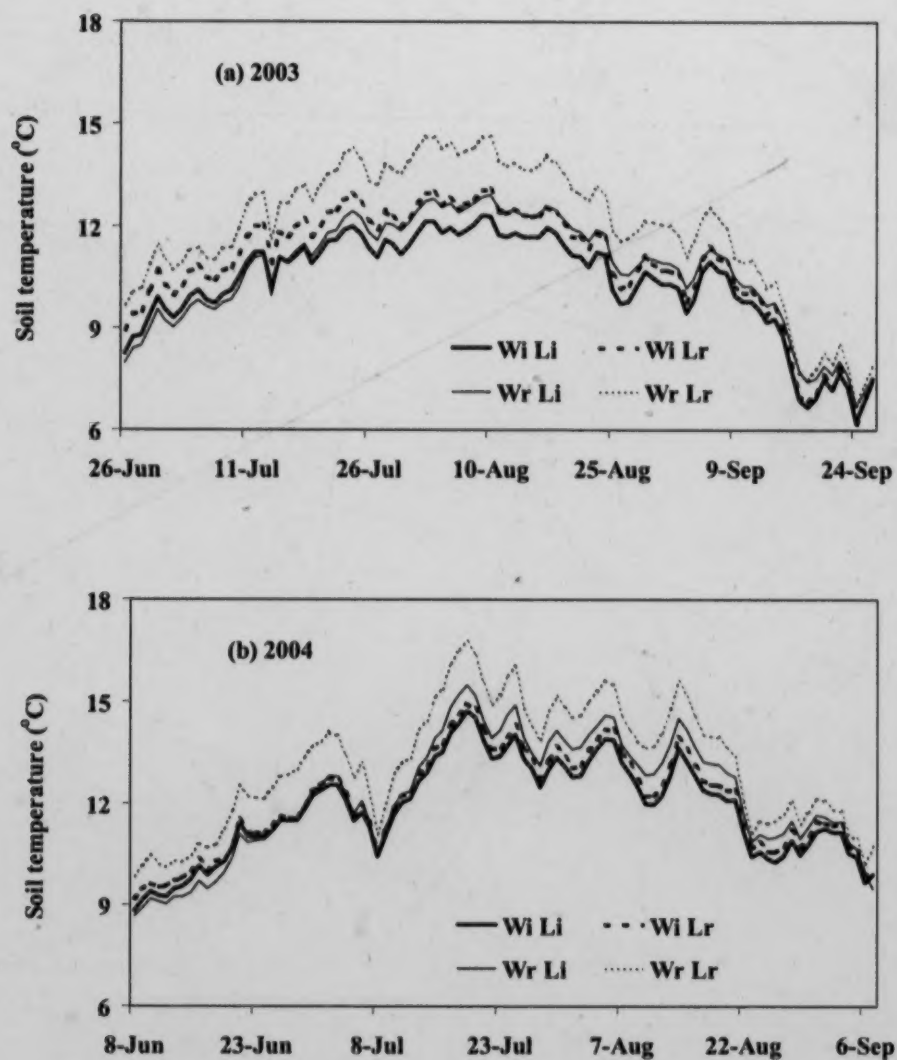


Figure 3.2 Gravimetric soil moisture content as affected by weed management, N fertilization, and litter removal. (a) LFH in 2003, (b) LFH in 2004, (c) mineral soil (0-10 cm) in 2003, and (d) mineral soil in 2004. The abbreviations are given in Table 3.3. Error bars are SEs.

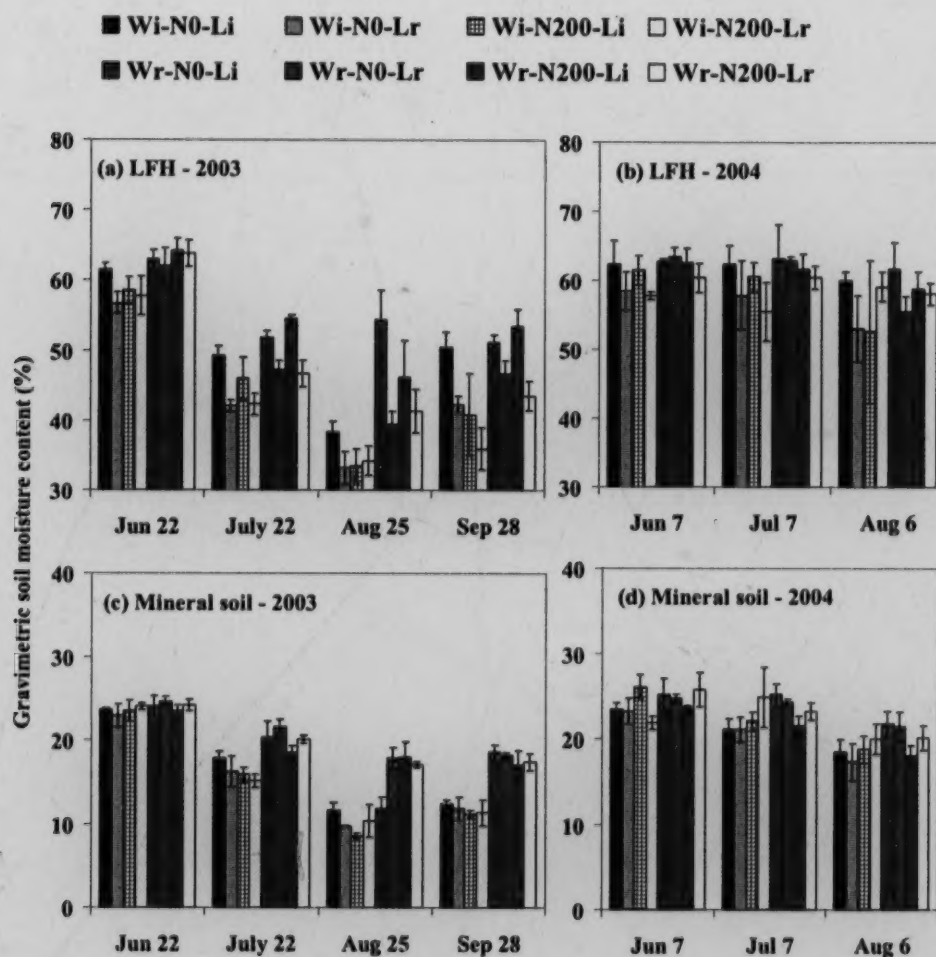
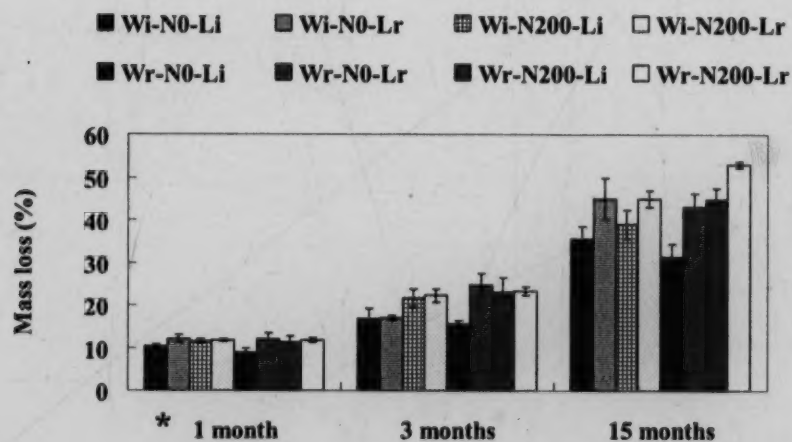


Figure 3.3 Rates of mass loss of bluejoint litter as affected by weed management, N fertilization, and litter removal. The abbreviations are given in Table 3.3. Error bars are SEs.



* "X month" means the length that a litter bag stayed on the ground. The litter bags were installed on June 22, 2004 and retrieved on July 22 (1 month) and September 28 (3 months) in 2003, and September 7 in 2004 (15 months).

Figure 3.4 Soil microbial biomass C as affected by weed management, N fertilization, and litter removal. (a) LFH in 2003, (b) LFH in 2004, (c) mineral soil (0-10 cm) in 2003, and (d) mineral soil in 2004. The abbreviations are given in Table 3.3. Error bars are SEs.

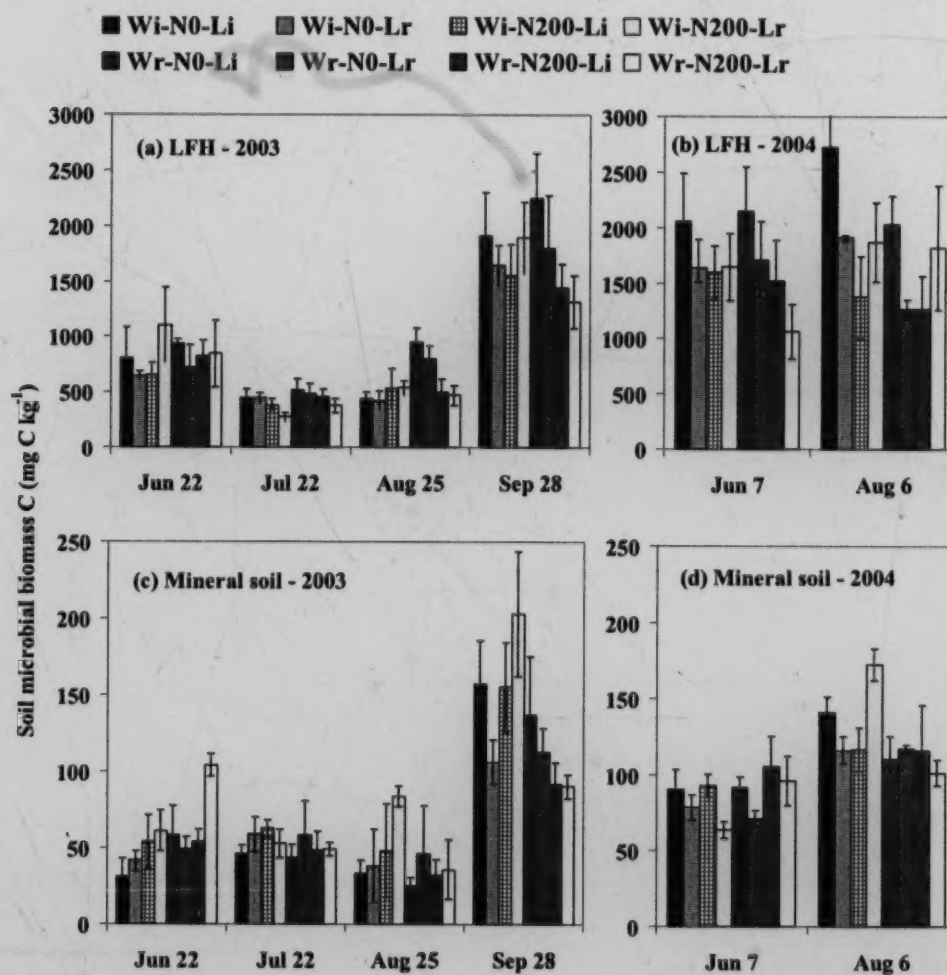


Figure 3.5 Soil microbial biomass N as affected by weed management, N fertilization, and litter removal. (a) LFH in 2003, (b) LFH in 2004, (c) mineral soil (0-10 cm) in 2003, and (d) mineral soil in 2004. The abbreviations are given in Table 3.3. Error bars are SEs.

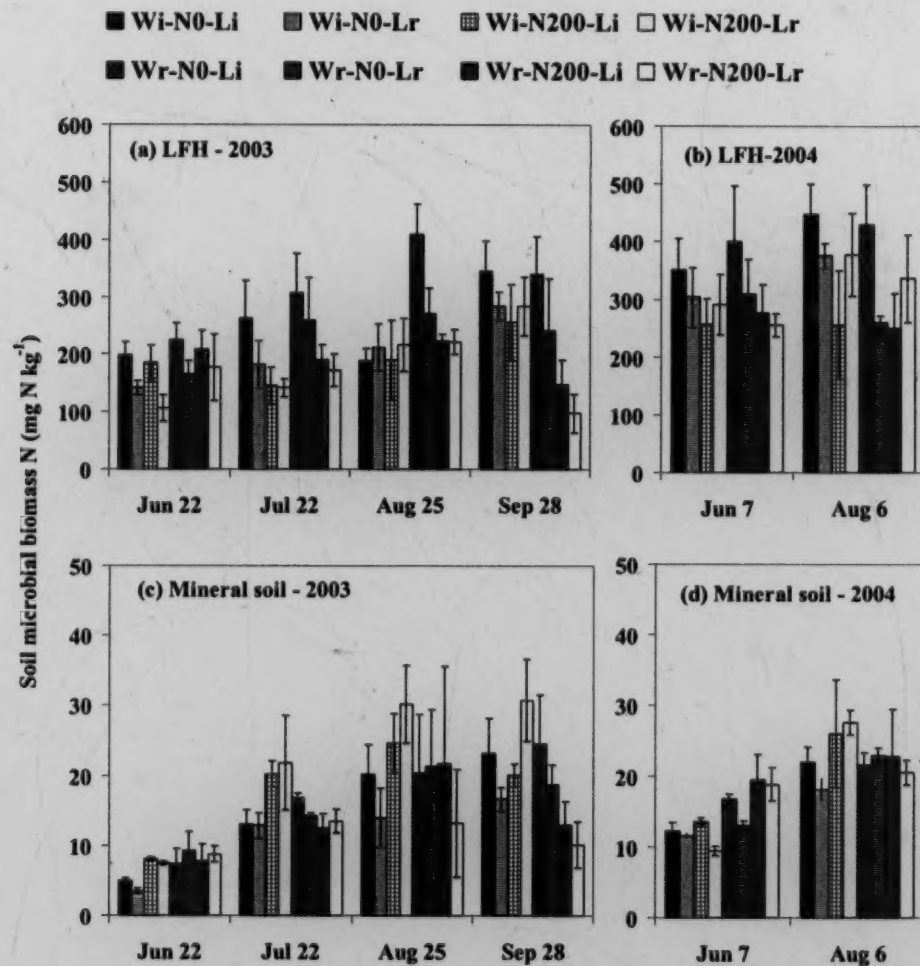


Figure 3.6 Net N mineralization rates as influenced by weed management, N fertilization, and litter removal in (a) LFH and (b) mineral soil (0-10 cm) in 2004. Abbreviations are given in Table 3.3. Error bars are SEs.

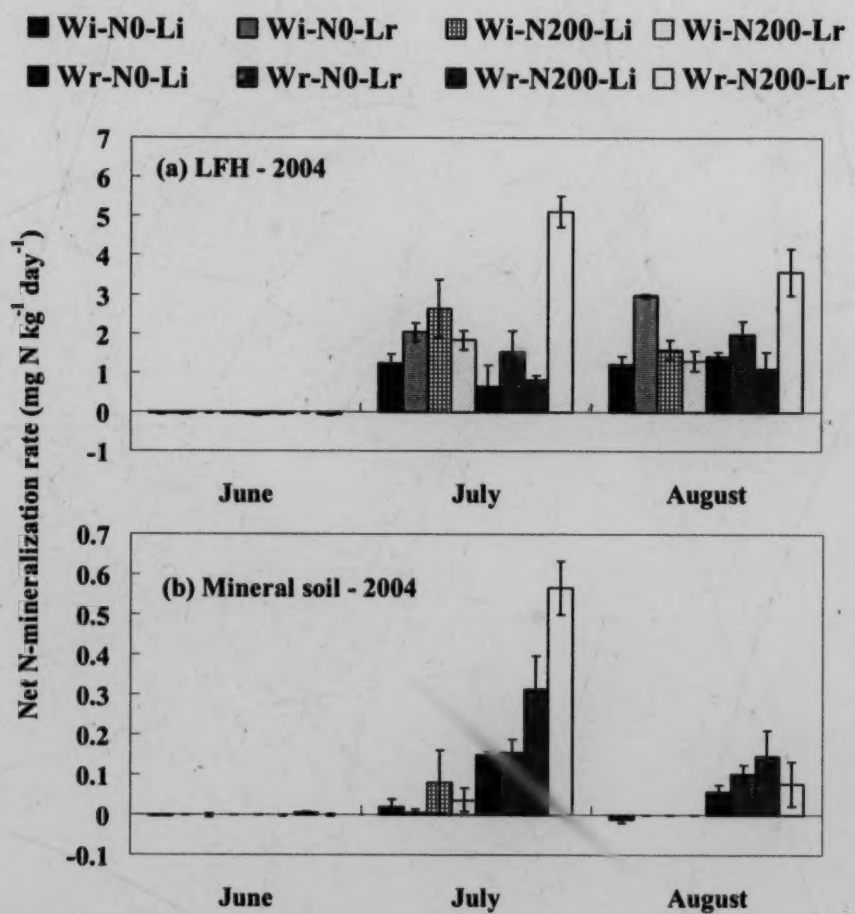


Figure 3.7 Net nitrification rates as influenced by weed management, N fertilization, and litter removal in (a) LFH and (b) mineral soil (0-10 cm) in 2004. Abbreviations are given in Table 3.3. Error bars are SEs.

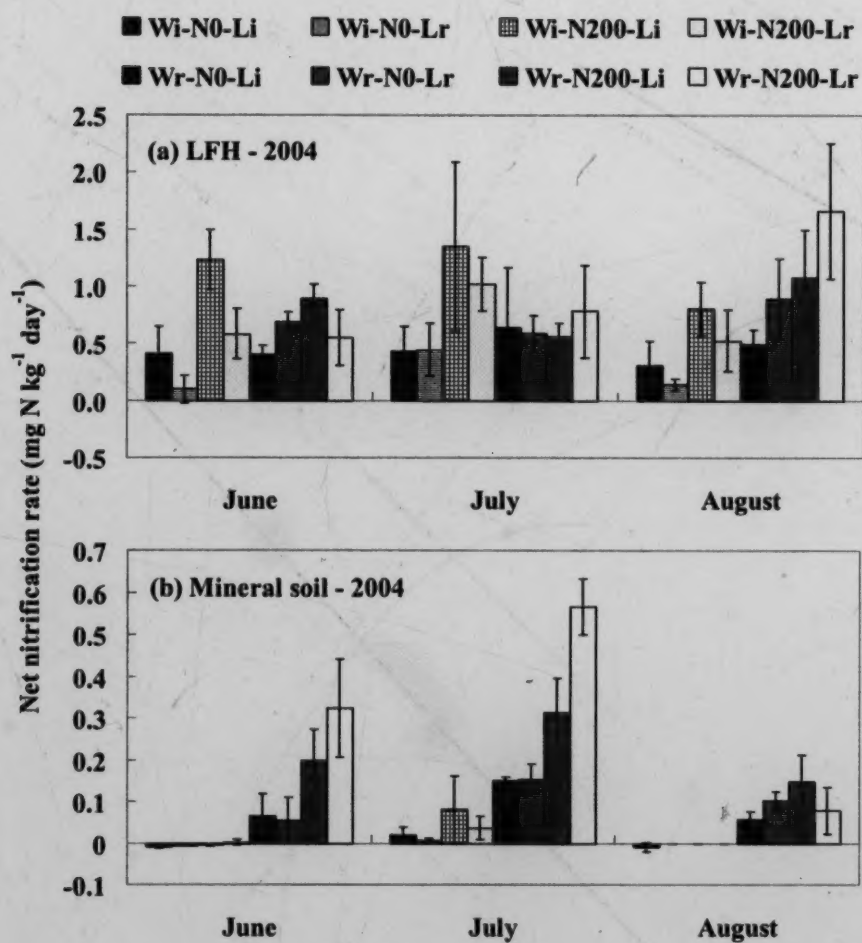


Figure 3.8 Correlations between net N mineralization rate and soil temperature in 2004:

(a) LFH and (b) mineral soil. Soil temperature is the mean value for each soil incubation period ($n = 72$; 24 plots x 3 replications in time).

● Wi N0 Li ■ Wi N0 Lr ▲ Wi N200 Li ◆ Wi N200 Lr
○ Wr N0 Li □ Wr N0 Lr △ Wr N200 Li ◇ Wr N200 Lr

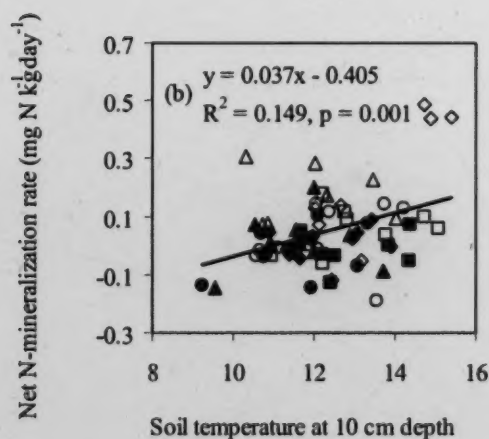
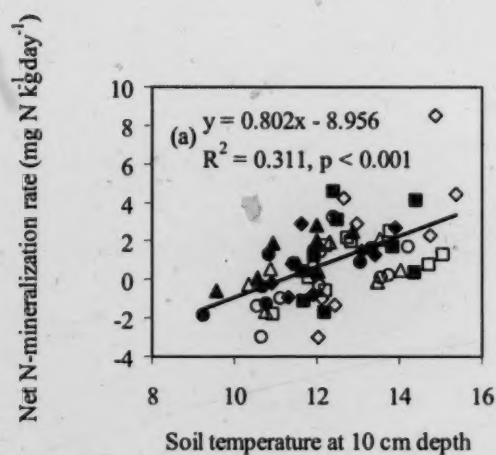


Figure 3.9 Soil NH_4^+ concentrations in (a) LFH in 2003, (b) LFH in 2004, (c) mineral soil (0-10 cm) in 2003, and (d) mineral soil in 2004. Abbreviations are given in Table 3.3. Error bars are SEs.

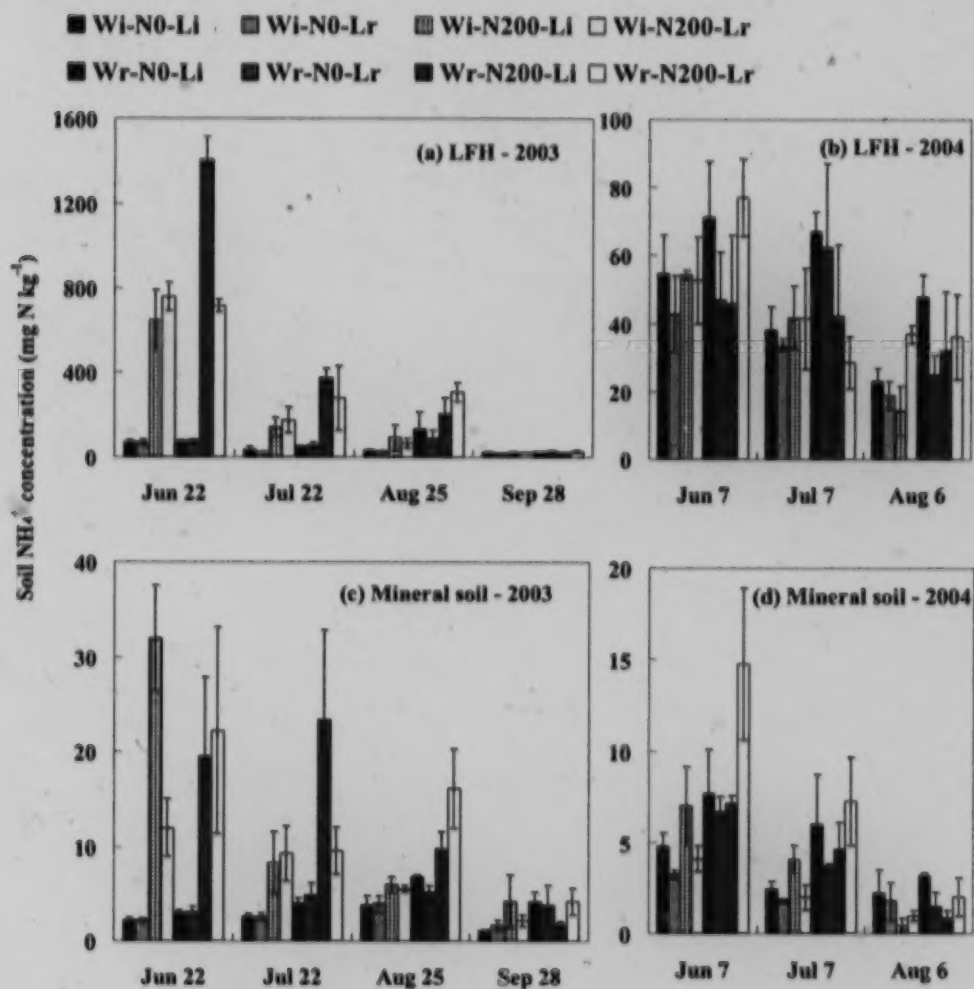


Figure 3.10 Soil NO_3^- concentrations in (a) LFH in 2003, (b) LFH in 2004, (c) mineral soil (0-10 cm) in 2003, and (d) mineral soil in 2004. Abbreviations are given in Table 3.3. Error bars are SEs.

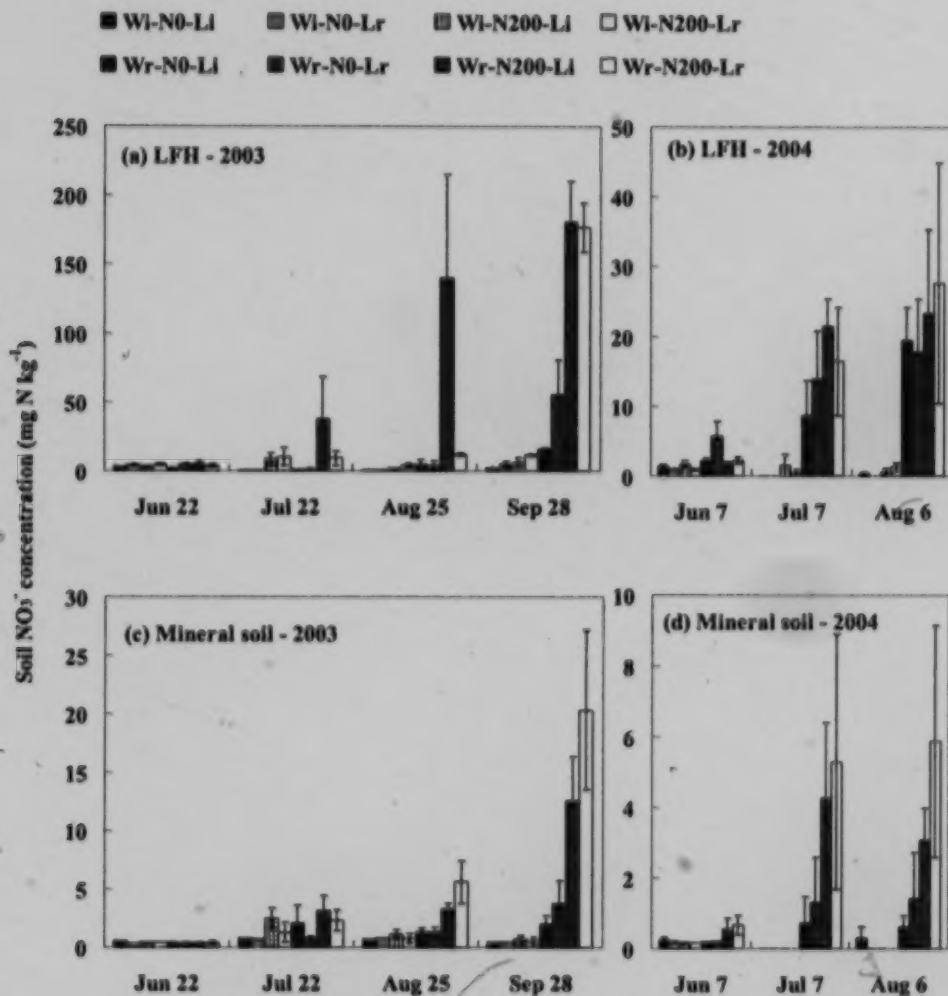
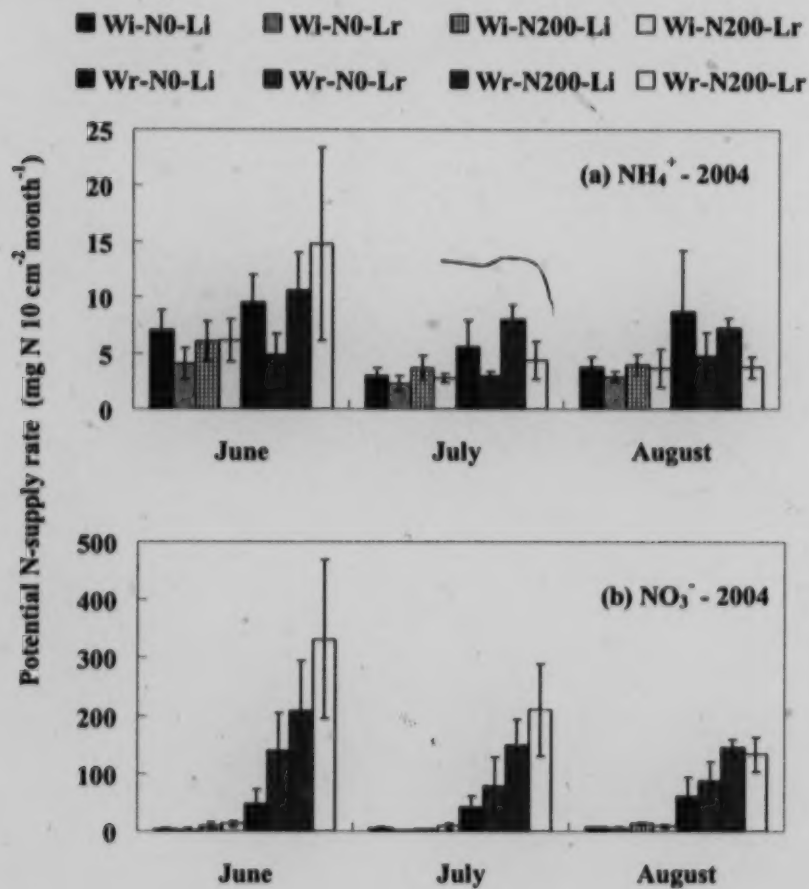


Figure 3.11 The potential rates of mineral-N supply measured by PRSTM-probes in 2004:

(a) NH_4^+ and (b) NO_3^- . Abbreviations are given in Table 3.3. Error bars are SEs.



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Chapter 4: Effects of weed control, N fertilization, and litter layer removal on the growth and nutrition of white spruce

4.1 Introduction

In boreal forests, detrimental effects of early successional vegetation on young trees in newly established stands have been widely reported (e.g., Bell et al. 2000). Canada bluejoint grass (*Calamagrostis canadensis* (Michx.) Beauv., hereafter referred to as bluejoint) is one of the most competitive herbaceous species in boreal forests and causes delay or failure of stand regeneration and economic losses to the forest industry (Eis 1981; Lieffers et al. 1993). The detrimental effects of bluejoint infestation on growth of white spruce (*Picea glauca* (Moench.) Voss) seedlings, an important commercial species in Alberta, have been reported (Eis 1981; Lieffers et al. 1993; Hangs et al. 2002). Two possible mechanisms for the strong competitive ability of bluejoint have been suggested: (1) cold soil temperature caused by a thick litter layer and standing dead shoots reduces tree growth rate (Hogg and Lieffers 1991; Landhausser and Lieffers 1998); (2) extremely high N uptake ability of bluejoint (Robinson et al. 2002; Hangs et al. 2002; Hangs et al. 2003a and 2003b) causes competition for the limited N supply in the soil. However, there is little discussion about tree growth reduction in relation to soil-N processes when affected by bluejoint, even though the importance of underground competition plays a critical role in controlling growth of target plant species (Nambiar and Sands 1993; Casper and Jackson 1997). In addition, most reports on bluejoint effects are based on pot experiments or field experiments conducted in stands less than 5 years after stand establishment.

Vector analysis is a tool that can be used to determine the direction and magnitude of tree response to fertilization and other silvicultural treatments such as weed control (Haase and Rose 1995). While several types of vector diagrams and their interpretation have been suggested (Timmer and Stone 1978; Timmer 1991; Imo and Timmer 1999), Mead and Mansur (1993) proposed a systematic interpretation for vector analysis to determine whether a tree is experiencing nutrient and (or) moisture deficiencies. In forest ecosystems, competition for nutrients and moisture often occur simultaneously (Nambiar and Sands 1993), and the interaction between these resources in ecosystem associated with bluejoint is not clear. Vector analysis by Mead and Mansur would be useful to separate these confounding effects of nutrients and moisture.

Three hypotheses were tested in this study: 1) weed removal increases tree growth as a result of reduced competition for N between weed and white spruce; 2) litter layer removal increases white spruce growth; and 3) fertilization improves white spruce growth. The objectives of this study were: a) to investigate the effects of bluejoint competition on white spruce growth in a 13-year-old stand; b) to examine the effects of litter layer removal and N fertilization on white spruce growth with and without bluejoint competition; c) to relate soil N processes with growth of white spruce; and d) to detect N deficiency of white spruce using vector analysis.

4.2 Materials and methods

4.2.1 Study site

The details of the study site and soil characteristics are described in Chapter 3.

4.2.2 Tree growth measurements

On June 5, 2003, every tree in each of the experimental plots was measured for height and diameter prior to applying the treatments. For tree diameter measurement, all trees were marked at 10 cm aboveground by a permanent marker and then measured using a caliper at two directions perpendicular to each other. The mean of the two measurements is the tree diameter. Tree height was measured using a height pole. Measurements were made again on September 28, 2003 and September 7, 2004. In 2004, diameter of some of the trees was measured on October 1 because of breakage of equipment, but that should have caused little effect on tree diameter comparisons among treatments because at that stage the trees had basically stopped growing. Tree growth was calculated by:

The 2003 growth = Value_{Sept 28, 2003} - Value_{June 5, 2003};

The 2004 growth = Value_{Sept 7, 2004} - Value_{Sept 28, 2003};

The 2003-2004 growth = Value_{Sept 7, 2004} - Value_{June 6, 2003}.

The average initial height and diameter of each experimental block are reported in Chapter 3; the overall average height was 181 cm and diameter was 3.7 cm.

4.2.3 Foliar growth and N concentration of white spruce and bluejoint

To perform vector analysis, fascicles of current year's growth were randomly collected from all trees in each experimental plot on September 28, 2003 and September

7, 2004. Aboveground biomass of bluejoint was collected in 20 x 20 cm quadrats from 3 randomly selected locations in each plot on September 28, 2003 and September 7, 2004. Plant samples were dried in an oven at 70 °C for 24 hours and weighed, and aboveground biomass of bluejoint was converted into 1 m² basis. Needles were separated from branches, and then 100 needles were randomly collected from each sample and weighed. The foliar samples were ground by a ball grinder (Retsch GmbH 88 Co., KG, Germany) and analyzed for total N concentration using a Shimadzu TOC-V CSH/CSN Total Organic Carbon Analyzer and the SSM-5000A Solid Sample Module (Shimadzu Corporation, Kyoto, Japan) in 2003. In 2004, the plant samples were digested using the Kjeldahl digestion method (McGill and Figueiredo 1993) and the N concentration in digests were analyzed using the Shimadzu TOC-V CSH/CSN Total N Analyzer (Shimadzu Corporation, Kyoto, Japan).

4.2.4 Vector analysis

Mead and Mansur (1993) suggested a systematic interpretation of vector diagrams to determine whether a tree is nutrient and (or) moisture deficient. The vector diagram and its interpretation are shown in Figure 4.1 and Table 4.1, respectively.

To depict a vector diagram that shows the treatment effects versus the control (Wi-N0-Li), the values of needle biomass, needle N concentration, and needle N content of each treatment were standardized as follows:

Standardized needle biomass, N concentration, and N content =

$$V_{\text{treatment}} / V_{\text{control}} \times 100$$

where $V_{\text{treatment}}$ is the value for Wi-N0-Lr, Wi-N200-Li, Wi-N200-Lr, Wr-N0-Li, Wr-N0-Lr, Wr-N200-Li, or Wr-N200-Lr, and V_{control} is the value for Wi-N0-Li.

A separate diagram was generated to show the effect of weed removal on tree growth and nutrition with the other two treatment levels fixed. In this diagram, the effects were depicted separately between the combinations of N fertilization and litter removal treatments; Wr-N0-Li was standardized by Wi-N0-Li to evaluate the effect of weed removal with no N fertilization and litter layer intact; Wr-N200-Li was standardized by Wi-N200-Li to evaluate the effect of weed removal with N fertilization and litter layer intact; Wr-N0-Lr was standardized by Wi-N0-Lr to evaluate the effect of weed removal with no N fertilization but litter layer removed; Wr-N200-Lr was standardized by Wi-N200-Lr to evaluate the effect of weed removal with both N fertilization and litter layer removed. Interpretation of the diagrams was according to Table 4.1.

4.2.5 Statistical analyses

The PROC MIXED procedure in SAS (version 8.2, SAS Institute Inc., Cary, N. C.) was used for analyzing the treatment effects on tree height and diameter growth, 100-needle weight, needle N concentration and content, and bluejoint biomass, N content and N concentration. The data in 2003 and 2004 were separately analyzed, except for tree height and diameter growth. Normality tests of the data set conducted by the PROC UNIVARIATE procedure and the Shapiro-Wilks test showed that all of the parameters were normally distributed. However, the Bartlett test by the PROC GLM procedure showed that the data had variances that were not homogenous. The PROC MIXED

procedure can properly handle this problem. Because the data had only 3 replications, it was suggested that there was not enough degrees of freedom to test more than 3-way interactions. Also, 3-way interactions can be difficult to interpret. Therefore, in the statistical model, only the main factors and 2-way interactions were included. For the statistical significance, $\alpha = 0.05$ was chosen.

The PROC REG procedure in SAS (version 8.2, SAS Institute Inc., Cary, N. C.) was used for the regression analysis to relate tree growth in 2004 (height and diameter) to mineral N supply rates or net N mineralization rates (see Chapter 3). For this analysis, the monthly mineral N supply rates or net N mineralization rates in June, July, and August in 2004 in each experimental plot was regressed against tree growth in 2004.

4.3 Results

4.3.1 *Tree growth response to the treatments*

Height growth was not significantly affected by any of weed removal, N fertilization, or litter removal treatments (Figure 4.2a). The effects were not consistent in the 2 years, and the differences among the treatments were relatively small. However, weed removal increased diameter growth in the 2-year study period ($p < 0.001$, Table 4.2; Figure 4.2b).

Figure 4.3 shows the correlations between NH_4^+ , NO_3^- , and mineral N ($\text{NH}_4^+ + \text{NO}_3^-$) supply rates, measured using PRSTM-probes (see Chapter 3), and tree growth increment in 2004. Tree height growth was not significantly correlated with the potential N supply rates. Diameter growth was correlated with the N supply rates. The R^2 value

was highest for the correlation between diameter growth and mineral N supply rates, followed by NO_3^- and NH_4^+ supply rates. Table 4.3 shows the R^2 and p values for the regression between growth increment (height and diameter) and the potential mineral N supply rates in each month of the 2004 growing season (June, July, and August). The R^2 values for the correlation between height growth and the N supply rate in any month were < 0.06 and non significant. Only diameter growth had significant relationships with N supply rates in each month of June, July, and August. For NH_4^+ supply rate, the highest R^2 value was found in June, followed by July, and August. For NO_3^- supply rate, the highest R^2 value was found in July, followed by August, and June. For mineral N supply rate, the trend was similar to the one for NO_3^- . Figure 4.4 shows the correlations between net N mineralization rates, measured using the buried-bag method, and tree growth increment in 2004. The relationship between diameter growth and net N mineralization rate in mineral soil was significant, but the correlations between diameter and mineralization rate in LFH, height and mineralization rates in LFH and mineral soil were not significant.

The weight of 100-needle of white spruce was reduced by weed competition ($p = 0.008$ in 2003, $p < 0.001$ in 2004, Table 4.2) (Figure 4.5a).

4.3.2 Tree and grass N concentration responses to the treatments

Weed removal and N fertilization did not affect needle N concentration in 2003, but both of them significantly increased needle N concentration in 2004 (Figure 4.5b). N content was significantly increased by weed removal in 2003 and 2004 (Figure 4.5c). Litter removal did not have any effect on N concentration or content.

The biomass of bluejoint in 2004 was lower compared with 2003 (Figure 4.6a). Nitrogen fertilization significantly increased biomass and N content of bluejoint in 2003 and 2004 (Table 4.2) and N concentration in 2003 (Figure 4.6a, b, and c). Litter removal did not significantly affect the biomass, and N concentration and content of bluejoint.

4.3.3 Vector analysis

The vector diagrams show the responses of trees to the treatments in 2003 and 2004. In 2003, only Wr-N200-Lr had greater tree growth and improved tree nutritional status compared with the control (Figure 4.7a). The other weed removal treatments improved needle N concentration of trees; N tended to be accumulated in trees (luxury consumption) under weed and litter layer removal and no N fertilization. In Wi-N200-Lr treatment, N fertilization did not improve tree growth; it even decreased tree growth in 2003. For Wi-N200-Li, the reason for this growth reduction based on vector diagnosis was moisture stress or in this case possibly salt stress induced by the treatment (Table 4.4). For Wi-N200-Lr and Wi-N0-Lr, the vector interpretation for these growth reduction was both moisture and N limitation caused by treatments. In 2004, the positive effects of weed removal were clearer than in 2003 (Figure 4.7b). All treatments of Wr in combination with the other 2 treatments improved tree growth according to Table 4.5. Nitrogen fertilization consistently had positive effects, but the magnitude of the effect was greater when weeds were also removed. Through 2003 and 2004, litter layer removal tended to improve tree nutrition and growth, but the lengths and directions were not consistent.

Figure 4.8 shows the response of trees (tree growth and nutritional status) to

weed removal since the control is W_i and respective N and litter treatments. The interpretation is in Table 4.5. The vectors of both diagrams are directed right and upward, and they indicate improved N and moisture availabilities through weed removal. But because the length of each vector was not consistent through 2003 and 2004, it is difficult to determine how N fertilization and litter removal interacted with the weed removal treatment.

4.4 Discussion

4.4.1 *Tree height and diameter growth*

The reduction in diameter growth of white spruce associated with bluejoint in the 13-year old stand indicates that competition can cause negative effects in an older stand, while previous studies were conducted mainly in younger stands (Robinson et al. 2001; Hangs et al. 2002). On the other hand, the lack of the effects of weed removal on height growth was consistent with the general observation that diameter growth is more sensitive to vegetation management than height growth (Sutton 1993). Weed management showed more obvious improvement in tree growth in the second year than in the first year. This result may be due to better control of weed in the second year of the experiment. Understory vegetation was controlled only by clipping in early June 2003, and there were new shoots emerging before herbicide was applied at the end of June, causing a delay in complete weed control. This may also have been related to that fact that white spruce is a determinate species, and the effect of first year weed removal was becoming compounded in the second year.

The significant correlations between the N supply rates and diameter growth of

white spruce indicate that N availability was one of the factors affecting tree growth in this stand (Figure 4.3). However, the R^2 values for the relationship between N supply rate and tree growth were relatively low compared with what is reported in Hangs et al. (2004). These low values may be due to the older trees with better-established root systems, which enable trees to search for N more efficiently; the average rooting depth of similar aged white spruce is around 30 cm for small roots (Nadeau and Pluth 1997), while the roots of bluejoint are distributed between organic and mineral soil. Besides, tree growth may be controlled not only by N availability but also by other resource availabilities such as soil moisture which usually is the other major resource under competition (Nambiar and Sands 1993; Casper and Jackson 1997).

Based on the results shown in Table 4.3, the seasonal trend of N availability in relation to tree growth can be suggested: NH_4^+ availability in June explains a greater percentage of tree growth variation than that in July or August; NO_3^- availability in July explains a greater percentage of the variation in tree diameter growth than the ones in June or August.

4.4.2 Tree nutritional responses to the treatments

Consistent with previous studies (Hangs et al. 2003a), the removal of bluejoint significantly increased foliar N concentration and content of white spruce in this study (Figure 4.5b), indicating competition for N in weed intact plots. Nitrogen fertilization did not have any significant effect on tree growth and nutritional status in the absence of grass control. A study using ^{15}N -labeled controlled-release fertilizer (Hangs et al. 2003) concluded that bluejoint out-competed spruce seedlings for fertilizer N. Staples et al.

(1999) found that understory vegetation control increased the fertilizer-use efficiency of white spruce seedlings by limiting competition for N, indicating significant N uptake by understory species. In this study, substantial amount of fertilized-N was taken up by bluejoint, and N fertilization increased biomass and N concentration of bluejoint in the first year (Figure 4.6a, b, and c). As a result, N fertilization did not affect growth and nutrition of white spruce in this experiment.

4.4.3 Bluejoint responses to treatments

We found that mineral N, especially NH_4^+ concentration in the fertilized plots was decreased quickly after the fertilizer application (see Chapter 3). Previous studies showed that a significant amount of N applied in young forests was assimilated by understory species in the first growing season after application (Staples et al. 1999). In this study, bluejoint biomass in 2003 was greater than that in 2004 (Figure 4.6a). The effect of N fertilization on biomass of bluejoint was also much greater in 2003. Nitrogen fertilization significantly increased foliar N concentration of bluejoint in 2004 and N content in both 2003 and 2004 (Figure 4.6b and c). Fertilizer N may also be leached out of sub-surface soil and immobilized by microbes (Westbrook and Devito 2004). Prescott et al. (1995) reported that repeated N fertilization reduced the vigor and biomass growth of an ericaceous understory shrub species, salal (*Gaultheria shallon*). The fate of applied N in my stand is still not clear, and whether this same effect is occurring in bluejoint needs to be further tested.

4.4.4 Vector analysis

Vector diagrams are useful tool to detect tree responses (growth, nutrient concentration, and nutrient content) to silvicultural treatments, and their interpretation is based on the magnitude and direction of each vector (Haase and Rose 1995). While some interpretation tables only involve the interpretation for nutrient limitation (e.g., Timmer and Stone 1978), Mead and Mansur (1993) suggested a diagnosis interpretation for both nutrient and moisture limitations. In this study, the vector diagram shows that no treatment improved tree growth except for Wr-N200-Lr in 2003 (Figure 4.7a). Applied N fertilizer decreased tree growth and nutritional status when the weed growth was intact but litter layer was removed, indicating that fertilization induced greater competition for N between bluejoint and white spruce or induced salt stress to white spruce due to applied fertilizer with reduced moisture content because of litter layer removal. In 2004, the differences in tree growth and nutrition between the control and each respective weed removal treatment became larger than in 2003 (Figure 4.7b). Every vector, except for Wi-N200-Lr, showed that the treatments improved N and moisture availability. These vectors indicated competition for soil moisture between bluejoint and white spruce, even though significance of competition for N in plantations less than 5-year old stands has been emphasized (Robinson et al. 2001; Hangs et al. 2003). Nitrogen fertilization appears to be undesirable in stands heavily infested by bluejoint since the vector diagram showed decreased growth and needle N concentration and content of white spruce in weed intact and N fertilized plots (Figure 4.7a). The majority of applied N may be taken up by understory vegetation, and thus understory vegetation growth is promoted, causing further competition for N and moisture (Chang et al. 1996; Imo and Timmer 1999).

In a factorial experiment, the control point can be selected based on specific objectives of the analysis (Haase and Rose 1995). In Figure 4.8, the control was set as Wi plus the respective N fertilizer and litter treatments to evaluate the effects of weed removal. Each vector shows the effect of weed removal within each combination of the fertilization and litter treatments. In this study, weed removal improved tree growth and nutrition in combination with any of the other treatments (vector shift C), indicating substantial deficiencies of N and moisture for white spruce in the weed intact plots. Weed removal was most effective (had the longest vector) in the N200 and Lr combination for increasing tree growth and needle N concentration and content in both 2003 and 2004, which indicates the most intensive competition for N and water in Wi-N200-Lr. Litter removal decreased moisture content of LFH (see Chapter 3), but surface disturbance of vegetation was reported to stimulate sprouting and growth of bluejoint (Hernandes 1973). At the same time, litter removal combined with weed removal and N fertilization was an efficient way to increase tree growth and N uptake (Figure 4.2b and 4.6c).

Initially, litter removal was hypothesized to increase tree growth and nutrition since it would increase soil temperature (Hogg and Lieffers 1991). Increased soil temperature can directly improve tree physiology (Landhausser et al. 2001; Landhausser et al. 2003). However, in this study, increased soil temperature was hypothesized to increase net N mineralization and thus increase N uptake of trees. As described in Chapter 3, litter removal increased soil temperature; net N mineralization was positively correlated with soil temperature; and tree diameter growth was positively correlated with potential N supply rate (reflecting net N mineralization) (Figure 4.3). Litter removal tended to increase tree diameter growth (Figure 4.2b). However, the effects and shifts of vector diagnosis related to litter removal were inconsistent (Figure 4.2, 4.6, and 4.7).

This contradictory result was probably due to the complicated effects of litter layer on soil properties; i.e., litter removal not only can have a positive effect but also can have a negative effect on soil properties. For example, litter removal decreased soil gravimetric moisture content of LFH (see Chapter 3). Litter removal increased net N mineralization rate of LFH (probably due to higher temperature) but tended to decrease extractable C. Also, surface disturbance, which may be similar to litter layer removal effect, was reported to stimulate sprouting and growth of bluejoint (Hernandes 1973).

4.5 Conclusions

Tree diameter growth was significantly increased by removal of bluejoint, indicating that competition has negative effects on tree growth in the 13-year-old white spruce stand. Because the trees in this stands were taller than the grasses and there is little possibility that competition for light has impact on tree growth, belowground resource availabilities affected by competition are thought to play the most important role in this stand.

Since tree diameter growth was positively correlated with N supply rate measured using PRSTM-probes, N availability was one of the factors most affecting tree growth in the studied stand. In chapter 3, we found that bluejoint can influence soil N cycling through its N uptake, litter input, and accumulation of litter and standing dead biomass, which can affect soil temperature and soil microbial activities such as net N mineralization and nitrification. I can conclude that bluejoint causes negative effects on tree growth through changing soil N cycling and reducing N availability.

In terms of silvicultural treatments, applying herbicide was effective to control

bluejoint and thus improve tree growth in young white spruce stands. Removing accumulated litter layer of bluejoint may also improve tree growth because such removal can increase soil temperature and N availability. However, it should be noted that removing litter layer may reduce soil moisture availability at the same time. N fertilization can increase soil N availability and increase tree growth. N fertilization can also potentially stimulate weed growth as we observed negative effects of fertilization on tree growth where bluejoint was intact in the first year of the experiment.

Table 4.1. Interpretation of the vector diagram depicted in Figure 4.1 (after Mead and Mansur 1993).

Shift	Response of needles in:			Effects of treatments on tree:		
	Bio-mass	N conc.	N cont.	Growth	Nutrient supply	Moisture regime
A	+	-	0/+	Improved	Not limited/ dilution	Stress reduced
B	+	-/0	+	Improved	Increased availability	Stress reduced
C	+	+	+	Improved	Increased availability	Stress reduced
D	0	+	+	No change	Not limited/ accumulation	Not limited
E	-	+	0/+	Reduced	Not limited/ accumulation	Stress induced
F	-	+ / 0	-	Reduced	Not limited/ uptake reduced	Limited
G	-	-	-	Reduced	Limited	Limited
H	0	-	-	No change	Luxury consumption	Luxury consumption

Table 4.2 Analysis of variance (p values) for tree height and diameter growth over two growing seasons, 100-needle weight, needle N concentration, needle N content, and bluejoint biomass, N concentration, and foliar N content

Effect	Height (2-yr)	Diameter (2-yr)	100-needle		Needle % N		Needle N content		Bluejoint biomass		Bluejoint % N		Bluejoint N content	
			2003	2004	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004
Weed control (W)	0.149	<0.001	0.008	<0.001	0.216	<0.001	0.015	<0.001						
N fertilization (N)	0.313	0.375	0.848	0.906	0.201	0.020	0.154	0.407	0.011	0.025	0.132	0.031	0.001	0.030
Litter removal (L)	0.605	0.290	0.713	0.535	0.288	0.869	0.511	0.615	0.346	0.519	0.508	0.131	0.241	0.650
W*N	0.571	0.929	0.126	0.002	0.870	0.568	0.266	0.008						
W*L	0.407	0.399	0.201	0.424	0.787	0.744	0.350	0.628						
N*L	0.163	0.375	0.047	0.300	0.114	0.054	0.015	0.056	0.620	0.201	0.681	0.094	0.515	0.316

Table 4.3. R^2 and P values for the correlation between tree growth (diameter and height) and the potential mineral N supply rate, measured using PRSTM – probes, in each month for the growing season of 2004.

	Height		Diameter	
	R^2 value	p value	R^2 value	p value
NH₄⁺ vs. tree growth				
June	0.006	0.723	0.342	0.003
July	0.000	1.000	0.188	0.044
August	0.002	0.840	0.149	0.062
Jun + Jul + Aug	0.003	0.805	0.424	0.001
NO₃⁻ vs. tree growth				
June	0.044	0.351	0.481	< 0.001
July	0.031	0.407	0.632	< 0.001
August	0.047	0.310	0.603	< 0.001
Jun + Jul + Aug	0.054	0.298	0.634	< 0.001
(NH₄⁺ + NO₃⁻) vs. tree growth				
June	0.044	0.351	0.494	< 0.001
July	0.020	0.526	0.668	< 0.001
August	0.043	0.331	0.600	< 0.001
Jun + Jul + Aug	0.041	0.392	0.679	< 0.001

Table 4.4. Interpretation of vector diagrams depicted in Figure 4.7 (a) and (b), based on Table 4.1. Each interpretation is compared with control, Wi-N0-Li, thus indicating the effect of the respective treatment.

Shift	Growth Response	Interpretation	Treatments
2003 (Control = Wi-N0-Li): Figure 4.7 (a)			
G	-	Both N and moisture deficiencies limited tree growth	Wi-N0-Lr, Wi-N200-Lr
E	-	Only moisture stress was limiting tree growth.	Wi-N200-Li
D	0	N was slightly accumulated in trees.	Wr-N0-Li, Wr-N0-Lr, Wr-N200-Li
C	+	Both N and moisture availabilities were increased.	Wr-N200-Lr
2004 (Control = Wi-N0-Li): Figure 4.7 (b)			
C	+	Both N and moisture availabilities were increased.	Wi-N0-Lr, Wi-N200-Li, Wr-N0-Li, Wr-N0-Lr, Wr-N200-Li, Wr-N200-Lr
G	-	Both N and moisture deficiencies limited tree growth.	Wi-N200-Lr

Table 4.5. Interpretation of vector diagrams depicted in Figure 4.8 (a) and (b), based on Table 4.1. All interpretation is compared with the respective control, Wi-N0-Li for Wr-N0-Li, Wi-N0-Lr for Wr-N0-Lr, Wi-N200-Li for Wr-N200-Li, and Wi-N200-Lr for Wr-N200-Li, thus indicating the effect of weed removal under different N fertilization and litter removal treatment combinations.

Shift	Growth Response	Interpretation	Treatments
2003 (Control = Weed removed)			
D	0	N and moisture availabilities were not limiting.	Wr-N0-Li
C	+	Both N and moisture availabilities increased.	Wr-N0-Lr, Wr-N200-Li, Wr-N200-Lr
2004 (Control = Weed removed)			
C	+	Both N and moisture availabilities increased	Wr-N0-Li, Wr-N0-Lr, Wr-N200-Li, Wr-N200-Lr

Figure 4.1. Vector diagram to explain treatment (e.g., competition) effects as suggested by Mead and Mansur (1993). Each arrow represents the effect of competing species to trees. The interpretation of these vectors is presented in Table 4.1.

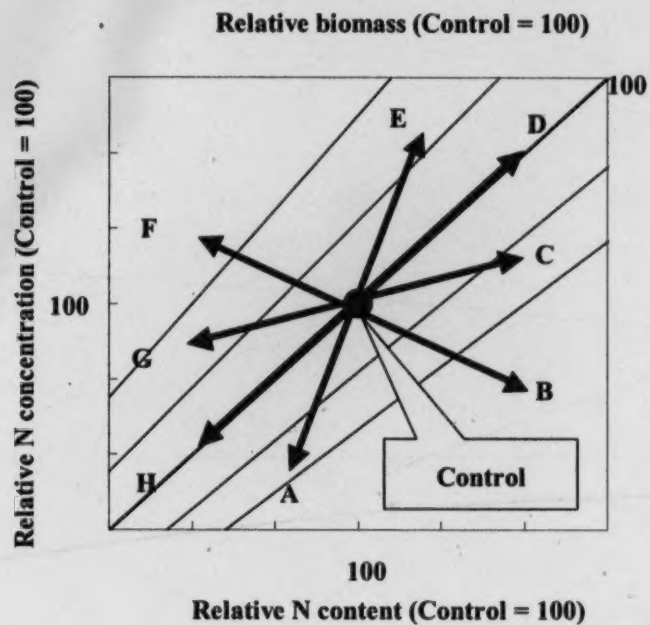


Figure 4.2 Effect of weed removal, N fertilization, and litter removal on a) tree height growth and b) diameter growth in 2003 and 2004. The growth of 2003-2004 is a summation of growth in 2003 and 2004. Error bars are SEs.

■ Wi-N0-Li ■ Wi-N0-Lr ■ Wi-N200-Li □ Wi-N200-Lr
 □ Wr-N0-Li ■ Wr-N0-Lr ■ Wr-N200-Li □ Wr-N200-Lr

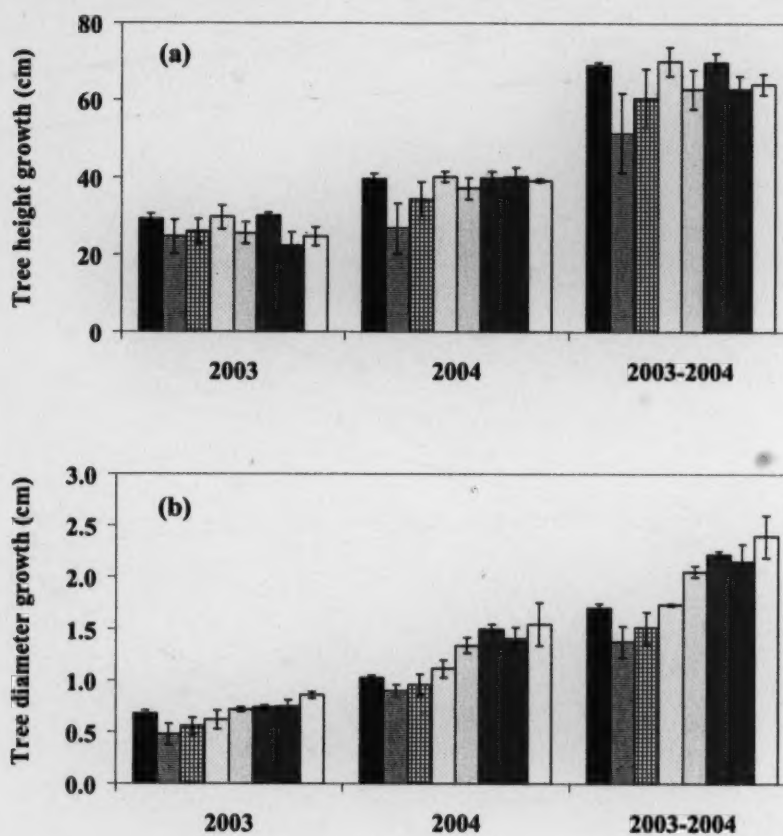


Figure 4.3 Regression of NH_4^+ , NO_3^- , and $(\text{NH}_4^+ + \text{NO}_3^-)$ supply rates, measured using PRSTM-probes, with white spruce growth increment (height and diameter) in response to weed removal, N fertilization, and litter removal. Mineral-N supply rates are the sum of the values of June, July, and August in 2004 in each experimental plot (n = 24).

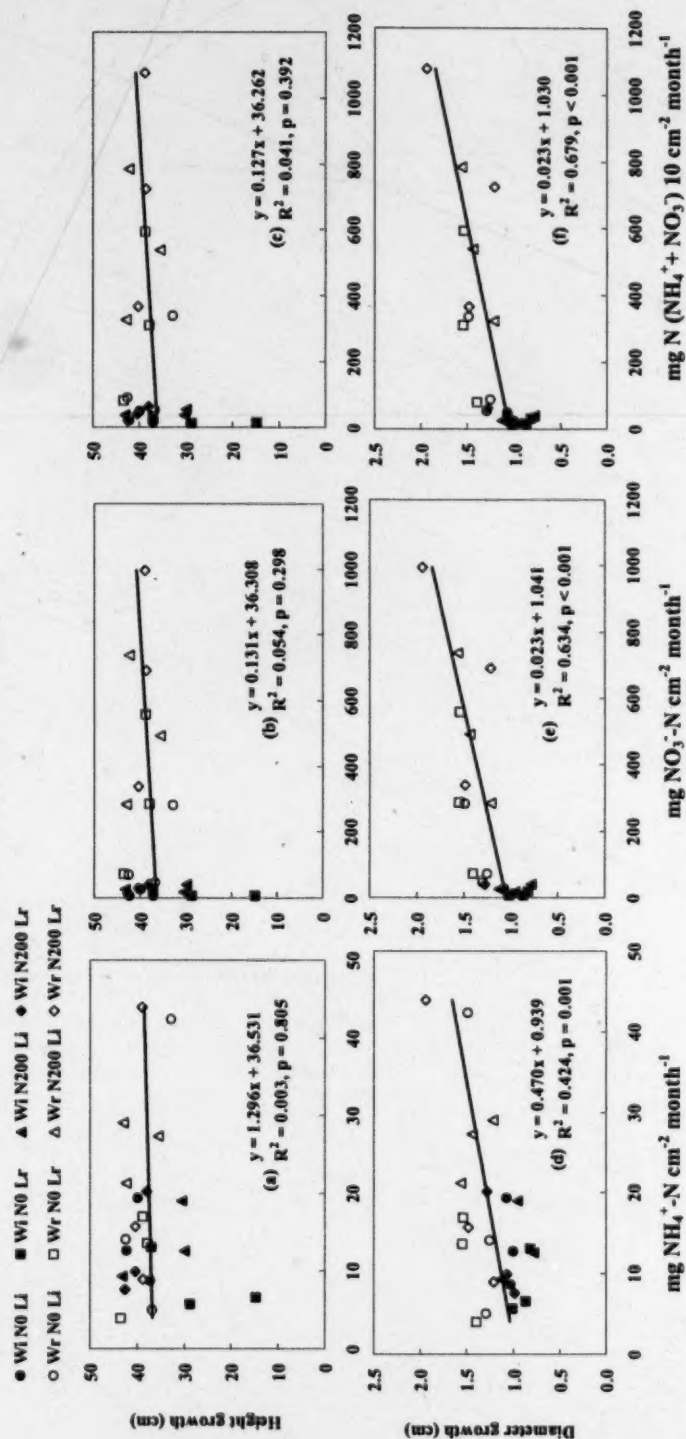


Figure 4.4 Regression of net N mineralization rates with the second-year (2004) growth increment of white spruce in response to weed removal, N fertilization, and litter removal. Net N mineralization rates are the sum of the values of June, July, and August in 2004 in each experimental plot (n = 24).

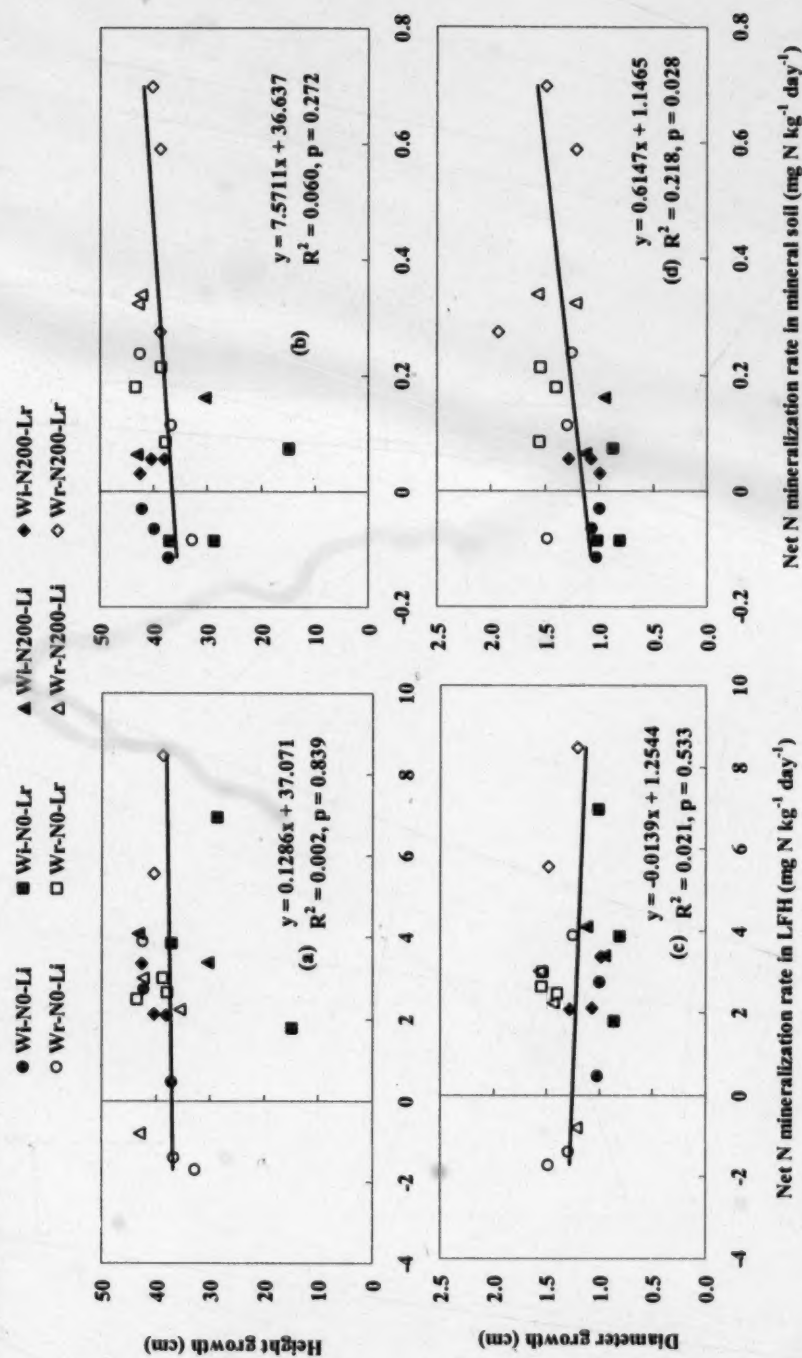


Figure 4.5 The effect of weed removal, N fertilization, and litter removal on (a) needle N concentration, (b) weight of 100-needle, and (c) N content in 100-needle of white spruce. Error bar are SEs.

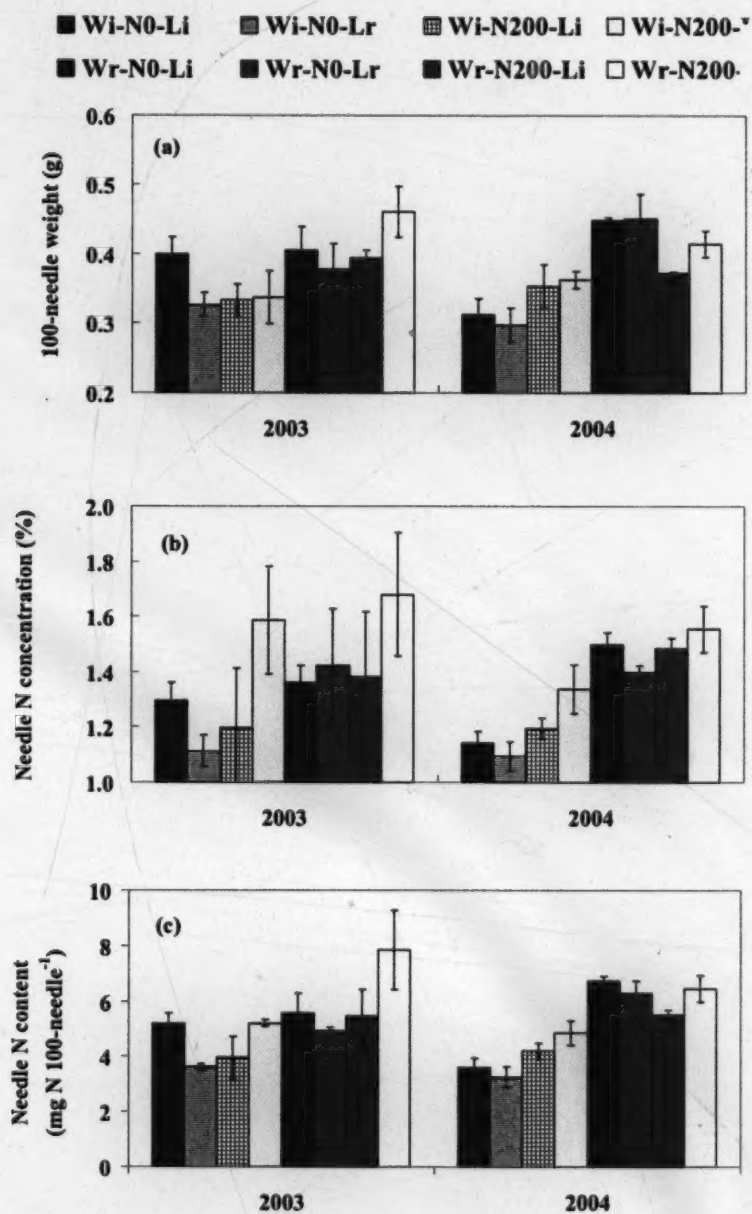


Figure 4.6 Effects of N fertilization and litter removal on (a) N concentration, (b) dry weight of biomass, and (c) N content of bluejoint. Error bars are SEs.

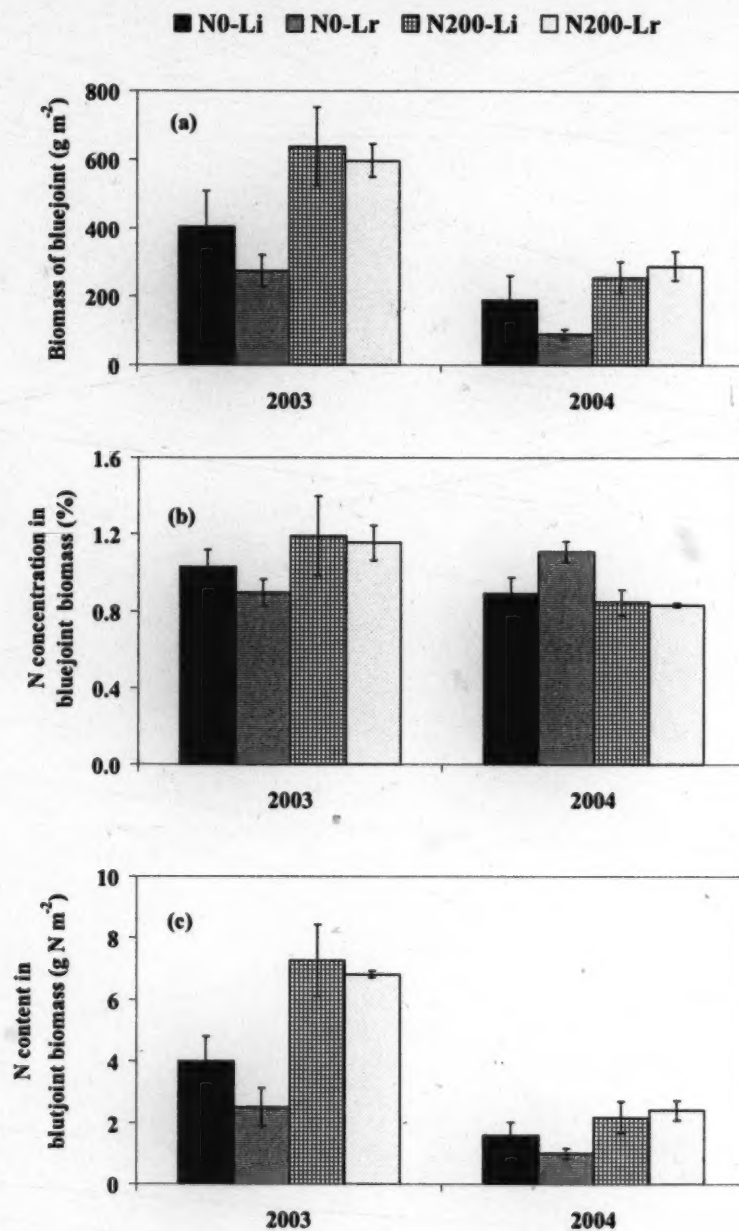


Figure 4.7 Vector diagrams showing the responses of trees to weed removal, N fertilization, and litter removal, as compared with the control: (a) 2003 and (b) 2004.

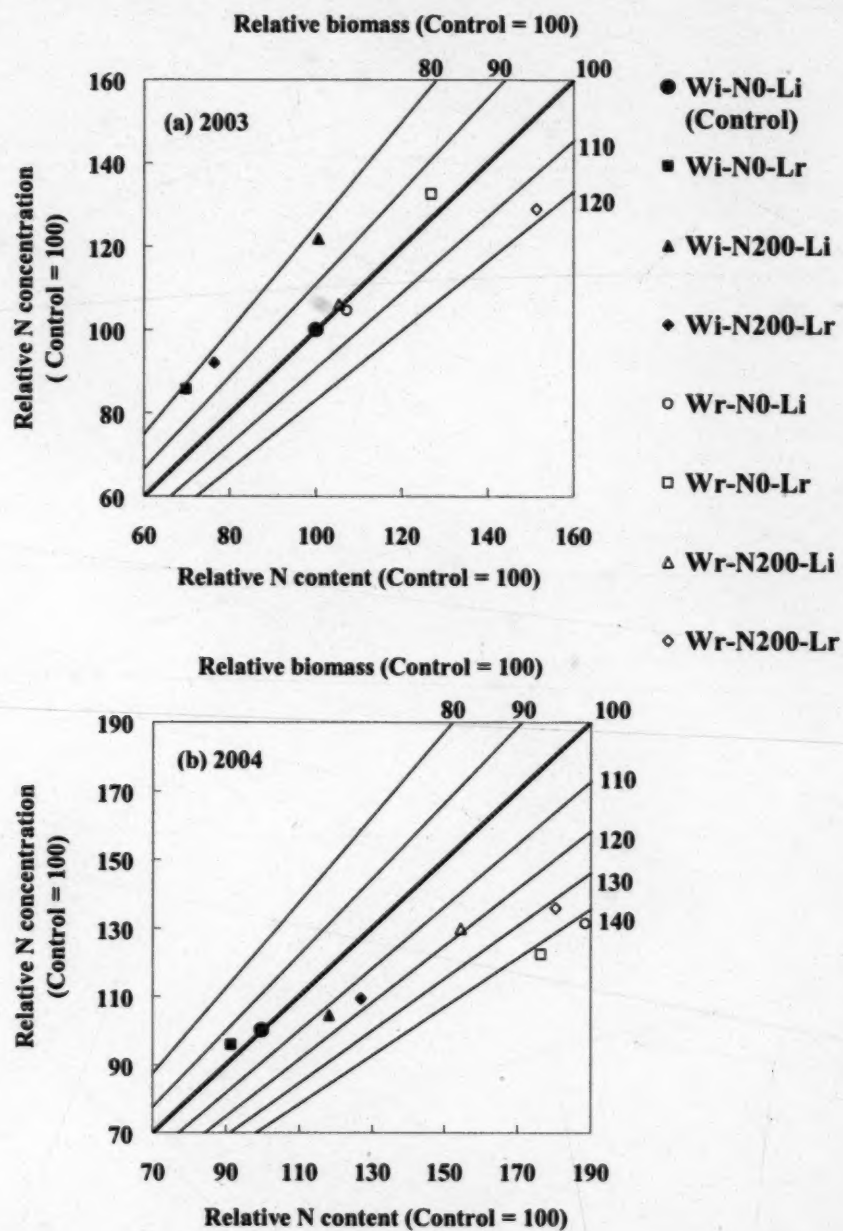
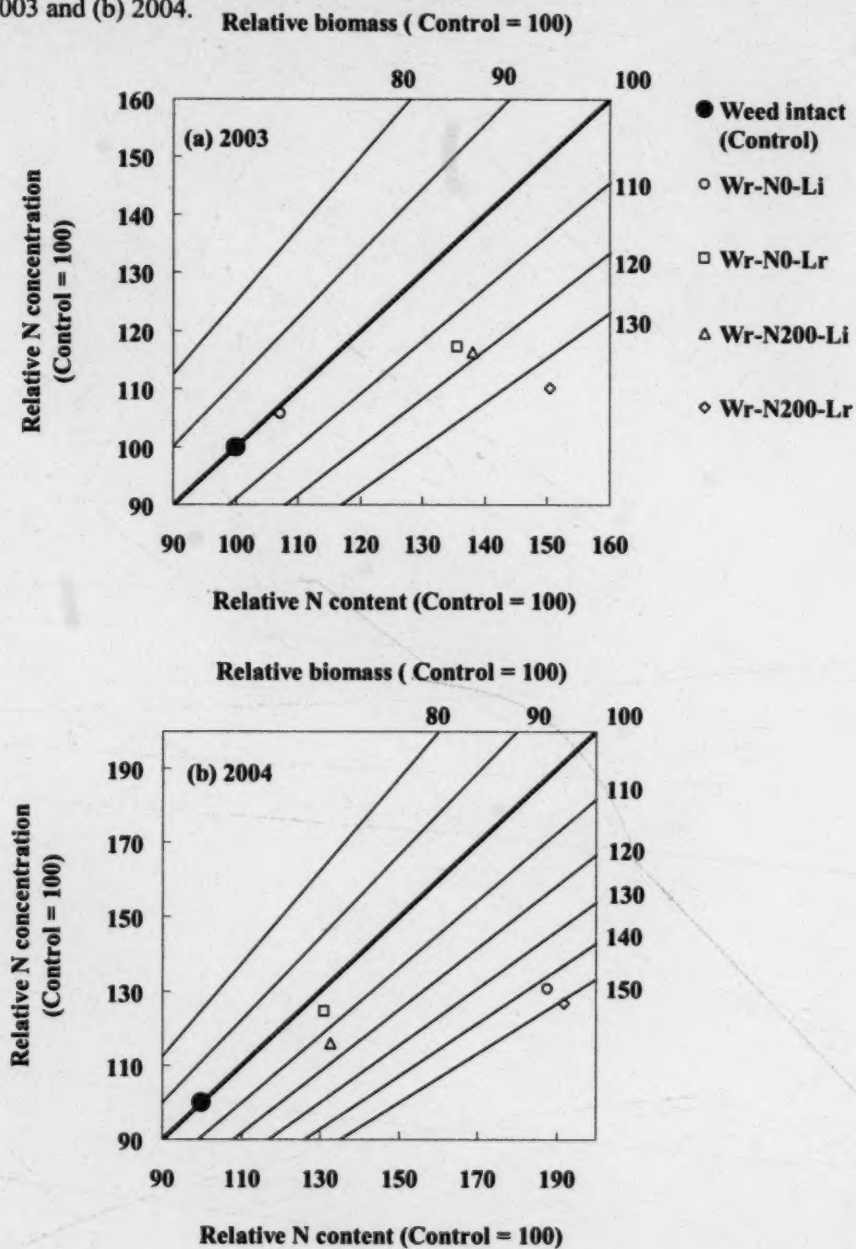


Figure 4.8 Vector diagrams showing the responses of trees to weed removal treatment only as compared with the control (keeping the other treatment levels the same): (a) 2003 and (b) 2004.



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Chapter 5: Does Canada bluejoint grass have a different effect on white spruce growth under different nutrient and moisture availabilities?

5.1 Introduction

Canada bluejoint grass (*Calamagrostis canadensis* (Michx.) Beauv., hereafter referred to as bluejoint) is typically found in mesic to hygric moisture and nutrient rich regimes in boreal forest (e.g., Eis 1981; Beckingham et al. 1996). Tree growth reduction caused by competition from this grass species in boreal forests has been documented (Lieffers et al. 1993; Ländhausser and Lieffers 1998; Bell et al. 2000). But whether high moisture regime, rich nutrient regime, or both of them facilitate the competitiveness of bluejoint is not clear, and the relationship between moisture and nutrient levels in affecting the growth of bluejoint is unknown. Interactions between soil moisture and nutrient availabilities are critical in influencing plant competition since soil moisture content affects mass flow and diffusion of nutrients in the soil that affect nutrient supply to plants (Casper and Jackson 1993). For example, Blank et al. (2002), in studying the mechanisms of competitiveness of *Lepidium latifolium*, which mainly invades wetland and riparian zones, found that biomass growth was facilitated under high soil water potential. They concluded that this species invades moisture-rich environments because high soil water content allows efficient transport of nutrients to the root system.

Considering soil moisture regime as a changing factor is important in relation to the predicted global climate change. In Canada, the mean annual precipitation over the last 40 years has been increasing (Akinremi et al. 1999), and the patterns of

precipitation events (e.g., light and heavy rain or storms) changing (Akinremi et al. 1999). The changed patterns of precipitation could lead to droughts or excessive wet periods (Easterling et al. 2000). Scientists have been trying to generate a quantitative insight into the fate of plant species and ecosystems that will experience climate change (Oswald et al. 2003). For example, a study by Fay et al. (2003) reported that the manipulation of the timing of rainfall (lengthened inter-rainfall dry intervals) reduced the aboveground net productivity of grassland. The reduction was due to decreased growth of subdominant grass species in the site while the dominant grass species did not respond to the manipulation; this result shows differences between plant species in sensitivities to precipitation change. Soil moisture regime change is an important factor in determining outcomes of plant competition that is affected by global climate change.

In this chapter, the main objective is to examine the effects of different N and moisture levels on competition between bluejoint and white spruce. It was hypothesized that bluejoint requires adequate water supply for its N uptake, and only when there is sufficient available water, bluejoint outcompetes trees for N. The specific hypotheses tested are: 1) soil N level, moisture level, and their interaction affect biomass, N concentrations, and N contents of trees and bluejoint; 2) the intensity of competition between trees and bluejoint is affected by N level, moisture level, and their interaction.

5.2 Materials and methods

5.2.1 Experimental design

This experiment was conducted in growth chambers from March to August in 2004. Three treatments were applied to 40 pots in a 2 x 2 x 2 factorial design with 5 replications (5 blocks). The treatments applied to the experiment are described in Table 5.1. Each block consisted of 8 seedlings of similar height. The location of a pot within a growth chamber was assigned by blocking. The 5 blocks were allocated to 2 growth chambers, with 3 blocks assigned to the first chamber and the other 2 blocks assigned to the second chamber. Within a block, the locations of the 8 pots were regularly rotated. The first treatment, competition level: Grass competition (GC) and no competition (NC), was assigned as tree seedlings associated with bluejoint and trees without bluejoint, respectively. The N fertilization treatment including two levels: a "high N" and a "low N" (higher and lower than the optimal) treatments suggested by Utriainen and Holopainen (2001). In their study, "high N" treatment increased N concentration and biomass of needles but was not toxic to trees. Nutrient solutions containing these levels of N and the other essential nutrients at the optimal level were applied to the pots. The nutrient concentration of each solution is shown in Table 5.2. The moisture level treatment was completed by adjusting moisture content to 20 and 40% of soil volumetric water content, where the volumetric water content at field capacity of growth media is around 50%. The concentration of nutrients in solution applied for the lower moisture regime was twice that of the one for higher moisture regime so that each pot receives the same amount of nutrients for the same fertility

treatment at each watering. Nutrient solutions were applied every 2 or 3 days to maintain soil moisture level at the desired levels. Reduction of soil moisture content, at each watering time, was detected using a Field ScoutTM TDR 100 Soil Moisture Meter (Spectrum Technologies, Inc., Illinois, USA) or by weighing the pot.

5.2.2 Plant collection and culture

The white spruce seedlings used in this experiment were containerized stock type PSB 412 1 + 0. The 32 seedlings (making up 4 of 5 blocks) were provided by the PRT Nursery in Beaverlodge, Alberta, and 8 (making up 1 block) by Coast to Coast Reforestation Nursery in Edmonton, Alberta. The seedlings were stored in a refrigerator (4 °C) until they were transplanted to pots on March 4, 2004.

Rhizomes of bluejoint were collected from the field experiment site (see Chapter 3) on September 28, 2003 and stored in a refrigerator (4 °C) until planting. After being washed with water to remove soil, rhizomes were cut into 5 cm pieces and planted in peat moss to germinate. About 30 days after germination, they were transplanted on April 24, 2004 to the pots with spruce seedlings that were assigned to the GC treatment, so that all pots had 4 to 5 shoots of bluejoint per pot.

Each pot (15 cm bottom diameter x 20 cm top diameter x 16 cm height) was filled with 700 g of a peat (Metro Mix 290) and vermiculite (Tettra Lite 2000) soil mixture (W. R. Grace & Co. of Canada Ltd, Ajax, Ontario). Nylon nets were placed in the bottom of the pots to minimize loss of growth media. The experiments were conducted in a controlled environmental chamber in the Department of Biological

Sciences, University of Alberta, where the conditions were maintained with a 18:6 h light:dark period, a day:night temperature regime of 24:15 °C, and a light level of 300 E s⁻¹ m⁻². When the experiment was halfway, bluejoint was found to require more light for its optimum growth, and the pots were moved to another growth chamber (16:8 h, 23:14 °C) that had more light (350 E s⁻¹ m⁻²) for about 60 days.

The 40 pots were watered to 45% of volumetric soil water content without any nutrients for 50 days, and then competition, N, and moisture treatments were applied for 114 days. At the end of the experiment, infestations of spider-mites were found on bluejoint shoots, and one of the blocks was heavily infested.

5.2.3 Plant measurements

The diameter and height of the seedlings were measured using a caliper and a tape measure on the day that treatment application started and after 114 days of treatment application. The increments of height and diameter were differences between these two measurements.

Aboveground bluejoint and current-year growth (flushed after transplanting) of white spruce were collected (hereafter referred to as current-year growth), dried in an oven at 70 °C for 24 hours, and weighed. Also, roots of white spruce were collected but not weighed since collection of roots was physically difficult due to complex root extension of bluejoint. Needles of white spruce were separated from branches, and then 100 needles from an experimental pot were counted and weighed. The shoots of bluejoint and needles and roots of white spruce were ground by a ball mill (Retsch GmbH 88 Co., KG, Germany) and analyzed for total N concentration using the

Kjeldahl digestion method (McGill and Figueiredo 1993) and the Shimadzu TOC-V CSH/CSN Total N Analyzer (Shimadzu Corporation, Kyoto, Japan).

5.2.4 Vector analysis

Mead and Mansur (1993) suggested a systematic interpretation for vector analysis to determine whether a tree is diagnosed nutrient and (or) moisture deficient. Their vector diagram and its interpretation are shown in Figure 4.1 and Table 4.1.

To depict a vector diagram that shows the effect of competition versus the control (no competition), the values of needle biomass, needle N concentration, and needle N content of each treatment were standardized based on the value of control as follows:

Standardized needle biomass, N concentration, and N content =

$$V_{\text{treatment}} / V_{\text{control}} \times 100$$

where $V_{\text{treatment}}$ is any value of GC-NH-MH, GC-NH-ML, GC-NL-MH, and GC-NL-ML. GC-NH-MH was standardized by NC-NH-MH; GC-NH-ML was standardized by GC-NH-ML; GC-NL-MH was standardized by NC-NL-MH; and GC-NL-ML was standardized by NC-NL-ML.

Interpretation of the diagrams was conducted using Table 4.1.

5.2.5 Statistical analyses

The proc MIXED procedure in SAS (version 8.2, SAS Institute Inc., Cary, N. C.) was used for analyzing: height and diameter growth, current-year biomass growth, 100-needle weight, needle N concentration, needle N content, and root N concentration of white spruce; and biomass, N content, and N concentration of bluejoint. Normality of the data set was tested by the proc UNIVARIATE procedure, and the Shapiro-Wilks test showed that every data set was normal. However, the Bartlett test conducted using the proc GLM procedure showed that the data had heterogeneous variances. The proc MIXED procedure overcomes this problem. For statistical significance, $\alpha = 0.05$ was chosen.

5.3 Results

5.3.1 Response of white spruce to competition, and N and moisture treatments

Tree height and diameter growth were significantly reduced by competition (Figure 5.1a and b; Table 5.3). The N and moisture levels did not influence tree growth as strongly as competition. Current-year biomass growth of trees was reduced by competition ($p < 0.001$), and it was significantly lower for NL than for NH ($p = 0.043$) (Figure 5.1c). Needles from NC were darker green-colored than the ones from the GC treatment. In agreement with this observation, the 100-needle weight was greater in NC ($p < 0.001$) than in GC (Figure 5.1d).

Needle N concentration was reduced by competition ($p < 0.001$) (Figure 5.2a).

The NH resulted in higher needle N concentration ($p = 0.001$), while moisture level had no significant influence. Nitrogen content per 100-needles was reduced by competition ($p < 0.001$), and the NH resulted in higher N content than the NL ($p = 0.005$) (Figure 5.2b). The moisture level did not affect N content. Root N concentration of white spruce showed similar trends to needle N concentration, and it was reduced by competition ($p = 0.003$) (Figure 5.2c). The observed spruce roots for the NC were more extensive and thicker than the ones in the GC treatment.

5.3.2 Response of bluejoint to N and moisture treatments

Bluejoint biomass was higher in the NH than in the NL treatment ($p < 0.001$) (Figure 5.3a); the NH treatment produced about twice the biomass as compared with the NL. A significant interaction between N and moisture levels was detected for aboveground biomass of bluejoint was found ($p = 0.007$). Within the NH treatment, moisture level did not change biomass, but the ML resulted in greater biomass than the MH. The NH also increased foliar N concentration and content for bluejoint ($p < 0.001$) (Figure 5.3b). The high level of N fertilization increased N content in bluejoint ($p < 0.001$), similarly to N concentration and biomass, but the moisture level did not affect N content of bluejoint (Figure 5.3c).

5.3.3 Vector analysis

Figure 5.4 shows the response of white spruce seedlings to competition with bluejoint under the 4 different combinations of resource availabilities. All the vectors

showed the G shift according to the interpretation (Figure 4.1), indicating competition caused reduction in tree growth regardless of N and moisture levels. The longest vector was observed for the NL-MH, followed by the NH-MH > NH-ML > NL-ML. The growth reduction was greatest in the NH-MH. The reduction in N concentration and content was greatest in the NL-MH.

5.4 Discussion

5.4.1 Response of white spruce to N and moisture treatments

Seedlings of white spruce planted or naturally regenerated in the boreal forest are often deficient in nutrients, so fertilization after planting usually improves their growth and nutrition (Nienstaedt and Zasada 1990). In this study, the applying elevated N level resulted in greater foliar N concentration, and N content in needles than the lower rate of N fertilization. A study that used the same N fertilization regime found that the NH was associated with significantly greater growth and nutritional responses of Norway spruce than the NL (Utriainen and Holopainen 2001). The foliar % N ranges from 1.0 to 1.4 (Figure 5.2a). The optimal foliar N concentration is 1.5 to 2.5% for white spruce (Nienstaedt and Zasada 1990), and the rate of fertilization used in this study was probably not sufficient for the seedlings of white spruce to achieve optimal growth. While the N level had significant effects on seedlings, the moisture treatment did not have any significant effects on white spruce seedlings. Silim et al. (2001) suggested that white spruce has a higher plasticity to drought as compared with other tree species. Water use efficiency increased when the seedling was in drought

condition, and there was less growth reduction due to drought (Silim et al. 2001). In this study, the low moisture treatment did not reduce white spruce seedling growth, but it is possible that the low moisture treatment may not be low enough to cause an immediate reduction in white spruce growth.

5.4.2 Response of bluejoint to N and moisture treatments

Bluejoint is known to prefer nutrient-rich sites (Lieffers et al. 1993). Robinson et al. (2002) found that bluejoint biomass significantly increased with the rate of N fertilization in a pot experiment. Results presented by Ländhausser and Lieffers (1998) were consistent with the above report. In this study, the biomass, N concentration and content of bluejoint were significantly larger in the NH treatment in this study (Figure 5.3a, b, and c). In contrast, the effects of the moisture treatment were not significant for those measurements. Bluejoint is known as a species that tolerates flooding conditions (Lieffers et al. 1993). Because growth of white spruce in poorly-drained conditions can be reduced, lowering water table by water uptake by bluejoint under poor drainage condition can be beneficial for white spruce in boreal forests (Ländhausser et al. 2003b). Bluejoint had the greatest leaf area when it was grown under water-saturated condition (Ländhausser et al. 2003a). On the other hand, Hogenbirk and Wein (1991) reported unchanged growth of bluejoint in response to drought. The volumetric moisture contents used in this experiment were 20% for the ML and 40% for the MH where the field capacity was around 50%. None of the pots was waterlogged. In this study, the moisture did not significantly affect the performance of bluejoint, except for the significant interaction effect between N and moisture levels on biomass, which

might be due to the concentration of N in soil solution in the NL-ML treatment. The growth of bluejoint was not affected by soil moisture availability within the range of moisture availability tested in this study. In general, bluejoint can be successfully established under sheltered and moist conditions (Lieffers et al. 1993). It should be noted that in this study the plants of bluejoint were sprouted from rhizomes and then transplanted to pots where the treatments were applied.

5.4.3 The effects of competition on white spruce seedlings

The white spruce seedlings associated with bluejoint exhibited significantly lower diameter, height, 100-needle weight, foliar N concentration, foliar N content, and root N concentration than competition-free seedlings (Figure 5.1 and 5.2). The aboveground biomass of bluejoint found in the NH was similar to that in the N fertilized plots for the first year of the field experiment (about 800 g m⁻²), and the one in the NL treatment was similar to in the un-fertilized plots (about 400 g m⁻²) (see Chapter 4). The density of plants was similar to previous studies conducted in boreal forests (e.g. Hangs et al. 2002). Therefore, the relative competitiveness affecting white spruce may be similar to the ones in the field. Reductions in tree growth or N uptake due to competition with bluejoint were also found in previous greenhouse studies (Robinson et al. 2002; Hangs et al. 2002) and field studies (Bell et al. 2000; Robinson et al. 2001; Hangs et al. 2003).

Robinson et al. (2002) observed that the negative influences of bluejoint on photosynthesis and N uptake of jack pine increased as N application rate increased. This result is consistent with the fact that bluejoint is frequently found in nutrient rich

sites (Lieffers et al. 1993); i.e., bluejoint can be more competitive where N availability is greater. In this study, the aboveground biomass of bluejoint was significantly higher in the NH (Figure 5.3a), and the reductions caused by competition in current year growth, 100-needle weight, and N content in 100-needle of white spruce were greater in the NH than in the NL treatment (Figure 5.1c and d, Figure 5.2b).

The acquisition of N can be an important determinant for trees under competition with bluejoint (Robinson et al. 2002). The ability of bluejoint roots to take up mineral N was reported to be much greater than that of white spruce (Hangs et al. 2003). The reduced growth, needle N concentration and content for the trees associated with grass are probably due to the high N uptake ability of bluejoint and thus reduced N availability for white spruce seedlings. Also, the length of white spruce roots can be reduced when they are grown with bluejoint (Hangs et al. 2002). In this study, the root biomass of white spruce associated with bluejoint was apparently smaller (not determined) and had lower N concentration (Figure 5.2c), implying that the extensive roots of bluejoint may inhibit the growth and N uptake of white spruce roots. The availability of moisture may be less important for competition between white spruce and bluejoint since the performances of white spruce and bluejoint were unaffected within the two levels of moisture treatments used in this study.

5.3.4 Vector analysis

The main objective of this experiment was to examine the effects of different N and moisture levels on competition between bluejoint and white spruce, and vector analysis may help explain those relationships.

The vector length shows the intensity of treatment effects (Haase and Rose 1995), and the NL-MH and NH-MH treatments had relatively intensive competition. For the NL-MH treatment, the reduction in growth was not greater than the other vectors, but the reductions in N concentration and content were largest. The vector for NL-ML showed a stronger reduction in growth but smaller reduction in N concentration and content. This result indicates that the relative effect of bluejoint competition on white spruce growth was greatest when availability of both N and moisture is low. The greatest reduction in tree growth caused by competition was observed in the NH-MH treatment. As a result of large uptake of available N and water by bluejoint, white spruce seedlings might not be able to take up enough resources, thus reducing its growth.

5.5 Conclusions

We observed no significant effects of manipulated moisture level (20 vs. 40% of volumetric moisture content where field capacity was 50%) on growth, N concentration and content of white spruce seedlings and bluejoint. This result is consistent with previous reports of high plasticity or lack in response to drought for white spruce (Silim et al. 2001) and bluejoint (Hogenbirk and Wein 1991). However, bluejoint has been reported to frequently establish in moist sites (Liefers et al. 1993), and this experiment used transplanted seedlings of bluejoint that were already sprouted. Therefore, the very early establishment of the grass such as germination and sprouting may require moist condition, and once they have established their root system, they may be able to tolerate certain moisture deficient conditions.

Initially, bluejoint was hypothesized to require certain amount of water for its N uptake and competitiveness. The NH treatment resulted in greater aboveground grass biomass, N concentration and content than the NL treatment. However, moisture level or the interaction between N and moisture did not affect the performance of bluejoint. Tree growth affected by competition was also greater in the NH than in the NL treatment and did not show the effect of moisture level. Thus, N availability appeared to be the major limiting factor for both growth of bluejoint and white spruce.

The vector diagram suggested that the severest competition for N was observed under the NL-MH condition; the severe competition for both N and moisture was observed under the NH-MH. For the NL-MH, more available soil moisture may facilitate the competitiveness of bluejoint for limited N. This result may be an indication for the interaction between N and moisture availabilities on competition. Because of the best performance of bluejoint in the NH-MH among the four treatments, white spruce growth was most strongly reduced by competition in the NH-MH treatment.

Table 5.1 Treatments applied to the pot experiment and their abbreviation used hereafter.

Competition	N supply	Moisture availability
No competition (NC)	Insufficient N applied (N low: NL)	Insufficient moisture applied (moisture low: ML)
Grass competition (GC)	Sufficient N applied (N high: NH)	Sufficient moisture applied (moisture high: MH)

Table 5.2 Concentrations (mg L^{-1}) of mineral nutrient solutions used in the greenhouse experiment, following Utriainen and Holopainen (2001).

Nutrient	High N (NH)		Low N (NL)	
	Chemical	Elemental	Chemical	Elemental
NH_4NO_3	286	N = 100	71	N = 25
KH_2PO_4	44	K = 13; P = 10	44	K = 13; P = 10
KCl	71	K = 37; Cl = 34	71	K = 37; Cl = 34
$\text{CaCl}_2 \cdot 6\text{H}_2\text{O}$	219	Ca = 40; Cl = 71	219	Ca = 40; Cl = 71
$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	154	Mg = 15; S = 20	154	Mg = 15; S = 20
$\text{FeCl}_3 \cdot 6\text{H}_2\text{O}$	5	Fe = 1; Cl = 2	5	Fe = 1; Cl = 2
$\text{MnCl}_2 \cdot 4\text{H}_2\text{O}$	0.6	Mn = 0.2; Cl = 0.1	0.6	Mn = 0.2; Cl = 0.1
H_3BO_3	1	B = 0.2	1	B = 0.2
ZnCl_2	0.04	Zn = 0.02; Cl = 0.01	0.04	Zn = 0.02; Cl = 0.01
$\text{CuCl}_2 \cdot 2\text{H}_2\text{O}$	0.05	Cu = 0.02; Cl = 0.02	0.05	Cu = 0.02; Cl = 0.02
$\text{Na}_2\text{MoO}_4 \cdot 2\text{H}_2\text{O}$	0.07	Na = 0.01; Mo = 0.03	0.07	Na = 0.01; Mo = 0.03

Table 5.3 Analysis of variance (p values) for the growth increments of white spruce (height and diameter growth, current-year biomass growth, weight of 100-needle, needle N concentration and content, and root N concentration) and bluejoint (biomass, foliar N concentration, and content).

Effect	Height	Diameter	Current year biomass	100-needle weight	Needle % N	100-needle N content	Root % N	Grass biomass	Grass % N	Grass N content
Competition (C)	0.005	<0.001	<0.001	<0.001	<0.001	<0.001	0.003			
N level (N)	0.912	0.804	0.043	0.912	0.001	0.005	0.527	<0.001	<0.001	<0.001
Moisture level (M)	0.581	0.487	0.932	0.085	0.325	0.055	0.899	0.495	0.149	0.158
C*N	0.360	0.487	0.072	0.809	0.384	0.206	0.595			
C*M	0.632	0.574	0.755	0.809	0.376	0.502	0.894			
N*M	0.581	0.221	0.322	0.085	0.977	0.456	0.967	0.007	0.061	0.604
C*N*M	0.686	0.070	0.234	0.066	0.362	0.679	0.739			

Figure 5.1 The effects of competition, N level, and moisture availability on a) tree height growth (increment), b) diameter growth, c) current-year biomass, and d) 100-needle weight. Abbreviations of treatments are given in Table 5.1. Error bars are SEs.

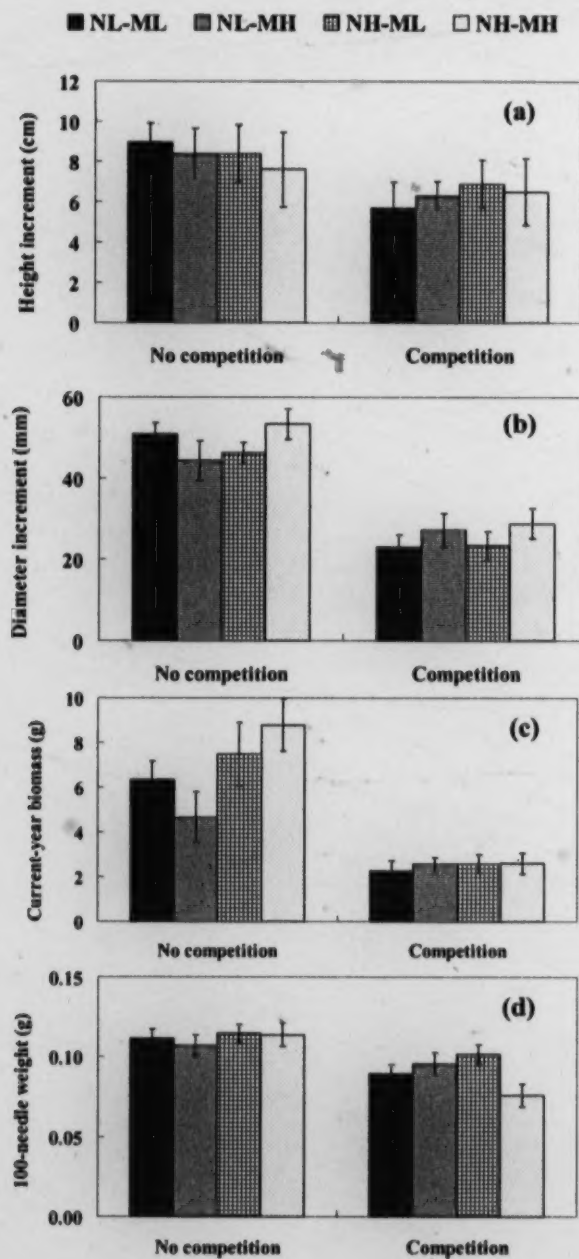


Figure 5.2 The effects of competition, N level, and moisture availability on a) needle N concentration, b) needle N content, and c) root N concentration. Abbreviations of treatments are given in Table 5.1. Error bars are SEs.

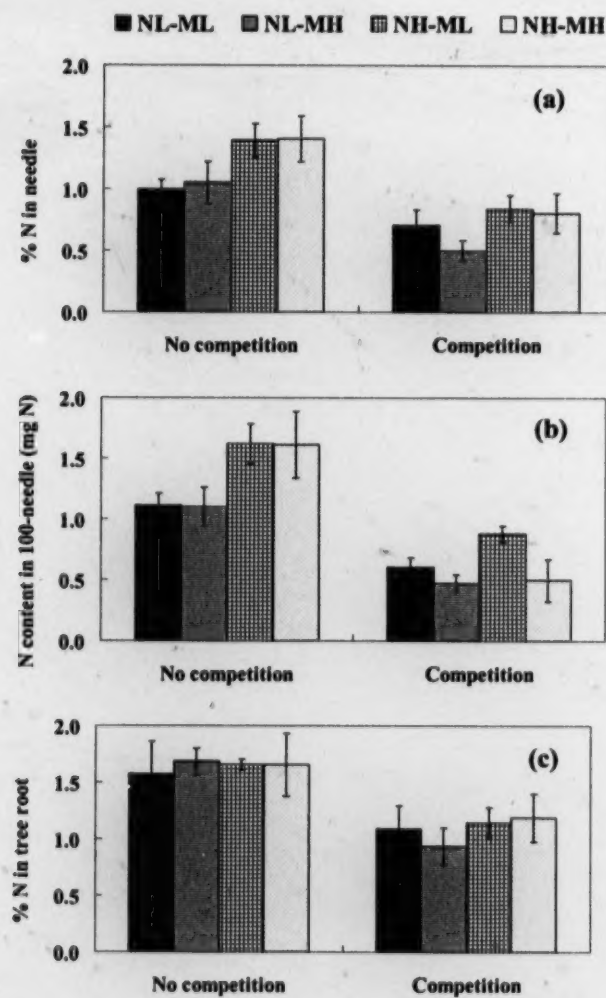


Figure 5.3 The effects of N level and moisture availability on a) aboveground biomass, b) foliar N concentration, and c) foliar N content of bluejoint. Abbreviations of treatments are given in Table 5.1. Error bars are SEs.

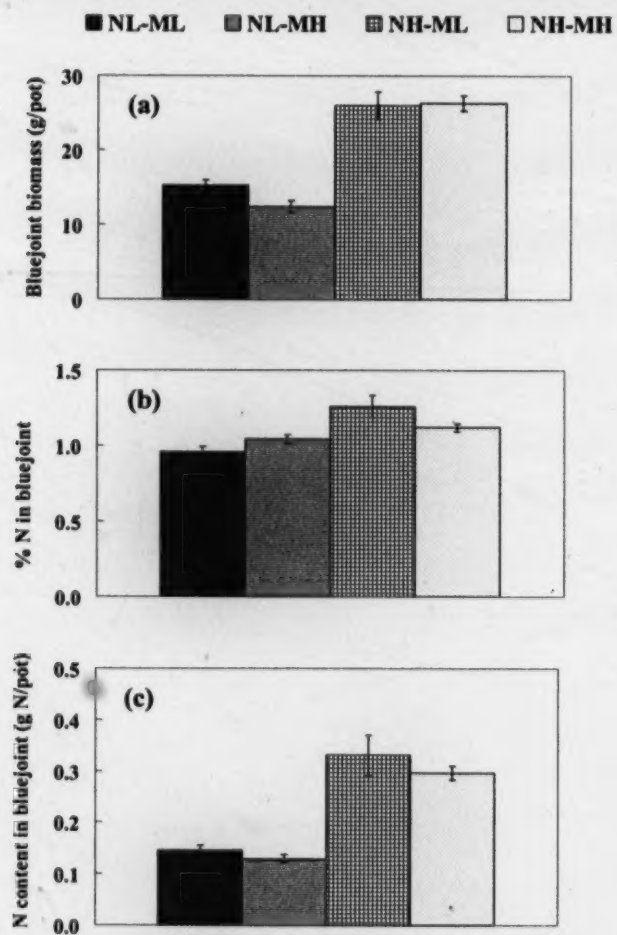
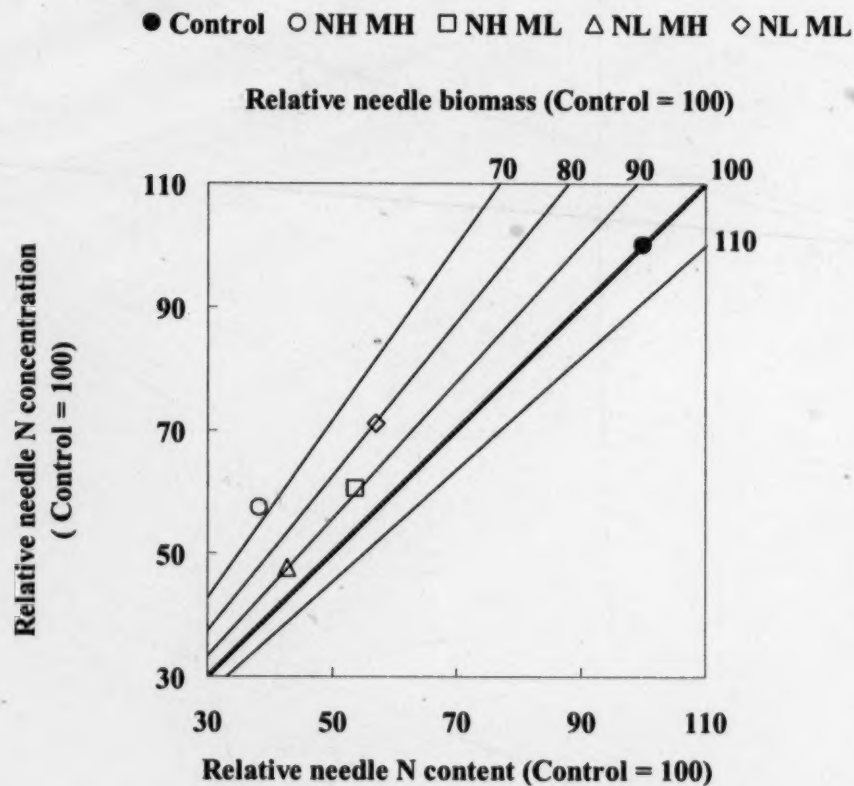


Figure 5.4 Vector diagram showing the responses of white spruce seedlings to competition with bluejoint under 4 different conditions: NH-MH (high N, high moisture), NH-ML (high N, low moisture), NL-MH (low N, high moisture), and NL-ML (low N, low moisture). Control represents the seedlings grown without competition under each of those conditions.



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Chapter 6: General discussion and conclusions

6.1 General discussion and conclusions

The main objective of this study was to examine the mechanisms of competition for belowground resources between Canada bluejoint grass (*Calamagrostis canadensis* (Michx.) Beauv., hereafter referred to as bluejoint) and white spruce (*Picea glauca* (Moench.) Voss) because bluejoint has been found to be a very competitive species in boreal forests (Lieffers et al. 1993). Another potential problem in systems with bluejoint infestation is the build up of a litter layer that decreases soil temperature (Hogg and Lieffers 1991) and that subsequently affects N cycling in the soil. Availability of belowground resources, such as N and moisture, can have strong influences on plant competition and growth (Casper and Jackson 1997). The following four hypotheses were tested in a field and a growth chamber experiment.

1. Bluejoint competes for N with white spruce and at the same time reduces net N mineralization and net nitrification rates in the soil, thereby reducing N availability and tree growth.
2. Nitrogen fertilization increases soil N availability and tree growth with or without vegetation control.
3. The litter layer of bluejoint reduces soil temperature, N mineralization rates, and N availability, leading to reductions in tree growth and N uptake.
4. Bluejoint requires a sufficient amount of available water for its optimal N uptake and for maintaining its competitiveness. Thus, when there is insufficient available water,

bluejoint becomes less competitive for N uptake. When soil water is sufficient, bluejoint out-competes white spruce even though there is insufficient nitrogen because of the extreme ability of bluejoint to take up N.

Based on the results from this thesis research, I can conclude the following:

1. Bluejoint competes for N and moisture in a 13-year-old planted white spruce stand.

Bluejoint reduced tree diameter and needle weight growth and reduced white spruce foliar N concentration and content. Vector analysis indicated that bluejoint competed for both N and soil moisture. Nitrogen fertilization significantly increased bluejoint growth and N concentration and content but did not affect the growth of white spruce. Bluejoint increased N uptake in response to increased N availability, consistent with other published studies (Robinson et al. 2001; Hangs et al. 2002; Hangs et al. 2003a).

A plant species can influence soil N processes and N availability through its unique biological characteristics (Scott and Binkley 1997; Scott et al. 2001; Knops et al. 2002) and in turn affects the ability of the species to compete with other species (Ehrenfeld 2003). Consistent with such generalizations, bluejoint was found to decrease soil N availability and in turn increase its competitiveness with white spruce, as summarized in Figure 6.1. For example, bluejoint infestation and the accumulation of a litter layer reduced soil temperature, which resulted in lower net N mineralization and nitrification rates. And tree diameter growth and N supply rates were positively related. Therefore, it can be concluded that bluejoint decreased soil N availability for white spruce because of competition for N and the reduction of soil temperature caused lower

net N mineralization rates; decreased N availability led to reduced white spruce growth.

2. Litter layer removal increased soil temperature and litter decomposition rate.

Litter layer removal significantly increased soil temperature, but its effects on net N mineralization and nitrification rates were not consistent. This is probably because litter layer removal also decreased soil moisture content which counteracted the effects of increased soil temperature on N mineralization and nitrification. Also, the decomposition constant of bluejoint litter was relatively low compared with other species based on data from the literature. In this study, the C:N ratio of bluejoint litter was relatively high (C:N = 63) compared with other woody and herbaceous species, suggesting the reason for the slow decomposition. The low litter decomposition rate allows the accumulation of a thick litter layer. Furthermore, the rates of litter decomposition significantly increased when litter layer was removed, probably due to increased soil temperature. Accumulation of litter and the concomitant decrease in litter decomposition rates due to low soil temperature and high litter C:N ratio may enable bluejoint to have longer mean residence time of N.

3. Nitrogen fertilization increased soil N availability when bluejoint was removed.

Nitrogen fertilization increased net N mineralization and nitrification rates, especially nitrification rates in mineral soil, particularly when vegetation was removed. Nitrogen fertilization increased foliar N concentrations in 2004 but did not significantly improve tree growth except for. Available N concentrations decreased faster when bluejoint was intact than when bluejoint was removed. In the mineral soil, weed control and N fertilization interactively affected nitrification rates: N fertilization did not increase

nitrification rates when the vegetation was intact but when weed was removed. There is a possibility that bluejoint obtained a large proportion of the applied N, which was supported by what was reported in Hangs et al. (2003b). The fate of applied N should be investigated on sites infested by bluejoint (discussed below).

4. Moisture availability did not affect the competitiveness of bluejoint. The importance of bluejoint competition for N was confirmed in the growth chamber experiment.

The growth chamber experiment tested the hypothesis that N and soil moisture availabilities affect the competitiveness of bluejoint. This hypothesis was not supported because the moisture availabilities used in the experiment did not affect the growth of bluejoint. This result was unexpected because bluejoint usually prefers moist sites (Lieffers et al. 1993). On the other hand, Hogenbirk and Wein (1991) reported unchanged growth of bluejoint in response to drought. The response of bluejoint to modified soil moisture availability should be tested with a wider range of availability and with non-organic material as growth media in future studies, for the better control of soil moisture status as a treatment.

Although the mechanisms of competition for N in relation to soil moisture availability are still not clear, I found that white spruce diameter growth and biomass production were reduced under competition with bluejoint, and this reduced growth and lower N concentration occurred simultaneously. Thus, the importance of competition for N, indicated by the field experiment, was confirmed by the growth chamber experiment. Also, vector analysis found that higher N availability introduced more intensive competition. Increased growth and N uptake of bluejoint in response to greater N availability has also been reported by Robinson et al. (2002).

6.2 Suggestions for future research

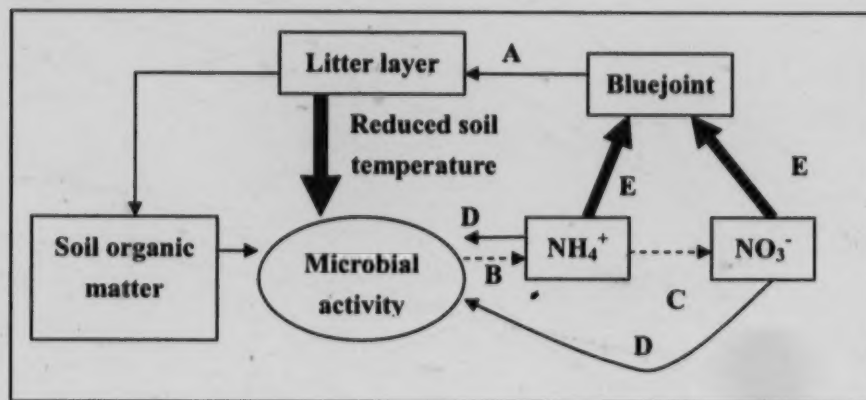
Based on vector analysis, N fertilization with intact bluejoint decreased tree growth in the first year of the field experiment. On the other hand, bluejoint biomass and foliar N concentration positively responded to N fertilization. Therefore, fertilization intensified the competition of bluejoint in the field. Previous studies using ^{15}N tracer have shown that understory vegetation can account for the uptake of a significant amount of applied N (Preston et al. 1990; Staples et al. 1999), and Chang et al. (1996) found that fertilization stimulated the growth of understory vegetation and reduced crop tree N uptake. On the other hand, Prescott et al. (1995) reported that repeated N fertilization reduced the vigor and cover of understory shrub species. The effect of fertilization on the competitiveness of weeds remains contradictory. Since this study was only conducted for 2 years and the fertilizer N was only applied once, the impact of repeated N fertilization on bluejoint needs to be evaluated.

The responses to fertilization between the field and growth chamber experiments differ and may be explained by the importance of extended rhizomes in the field experiment for bluejoint competition for N. Nitrogen fertilization did not increase the competition of bluejoint in the growth chamber experiment, even though bluejoint biomass and N uptake responded positively to the higher N level. The growth chamber experiment provided bluejoint a limited rooting zone, while the rhizomes in the field could be very extensive, giving an advantage to obtain more N. Therefore, experiments using pots in the greenhouse can potentially underestimate the competitiveness of bluejoint for the applied N. To gain a better understanding of the effect of fertilization, further studies, especially field experiments, are needed to clarify the fate of applied N

and its effects on the competitiveness of bluejoint.

Another area for future studies can be the effects of the bluejoint root system on soil microbial activities. Soil microbial biomass C and N were not significantly influenced by bluejoint removal, but net N mineralization and nitrification rates were significantly higher where bluejoint was controlled by herbicide application. Interestingly, net release of NO_3^- occurred only where there was no activity of bluejoint, and net supply rates of NO_3^- , rather than NH_4^+ , were better correlated with tree growth. Therefore, NO_3^- can be an important resource of available N in ecosystems experiencing intense competition between trees and bluejoint. Studies need to be conducted to determine whether bluejoint inhibits nitrification.

Figure 6.1 A conceptual model that demonstrates the influence of bluejoint on soil N cycling. Bluejoint produces litter and builds up a thick litter layer (A), and this reduces soil temperature and consequently soil microbial activity, especially net N mineralization rate (B+C-D, where B is ammonification rate, C is nitrification rate, and D is rate of N immobilization) and nitrification rate (C). Certain amount of mineral N is taken up by bluejoint (E), and this possibly causes competition for NH_4^+ with pathway C (substrate limitation for nitrifiers).



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